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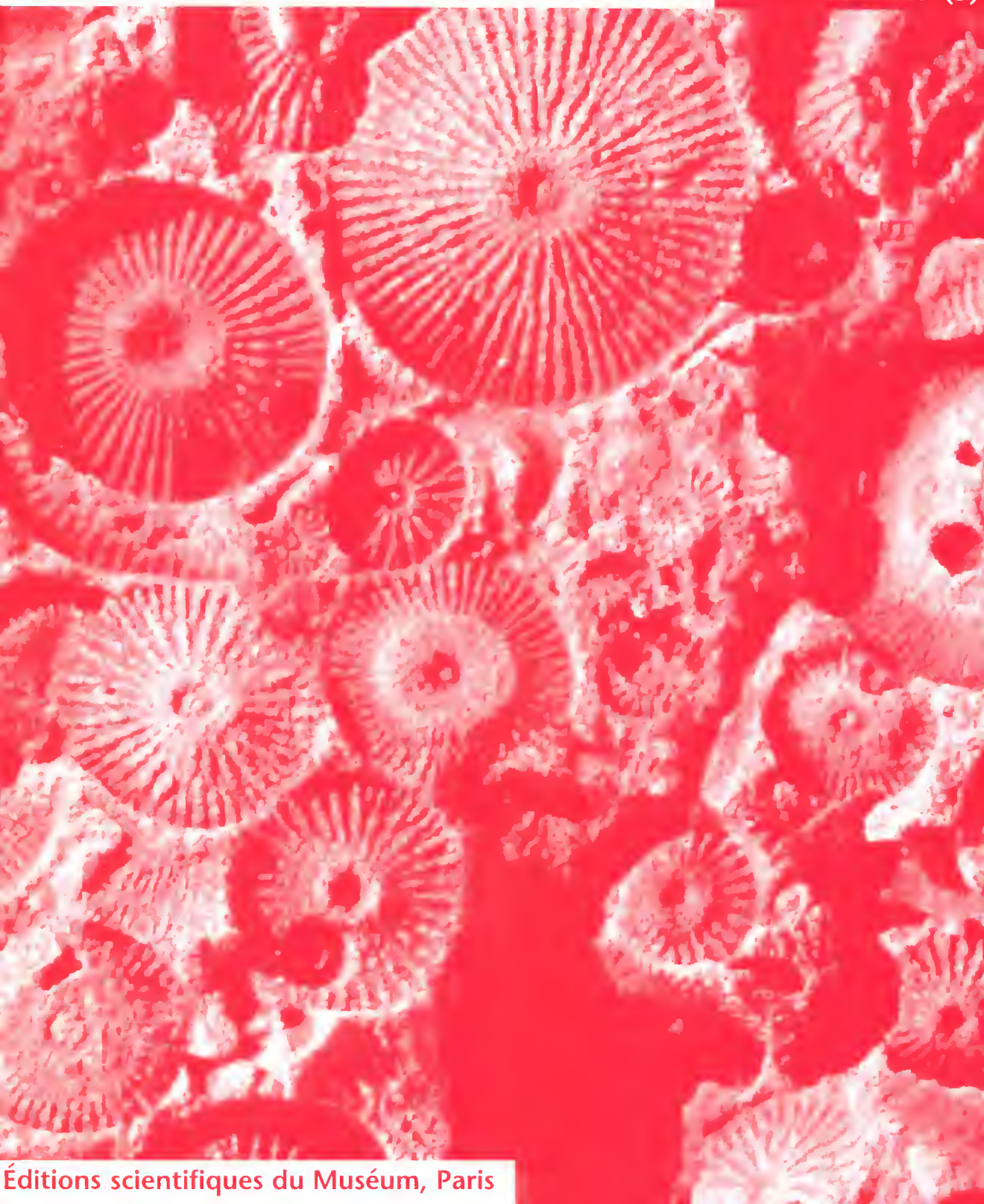

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Nouveaux poissons acanthodiens du Dévonien du Spitsberg

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Gagnier P.-Y. & Goujet D. 1997. — Nouveaux poissons acanthodiens du Dévonien du Spitsberg. *Geodiversitas* 19 (3) : 505-513.

RÉSUMÉ
Une description de deux nouvelles espèces de poissons acanthodiens est donnée. *Mesacanthus grandis* n.sp. est représentée par un spécimen articulé montrant bien les écailles du corps, les écailles modifiées de la tête et une scapula. *Xylacanthus minutus* n.sp. est représentée par une hémi-mandibule droite en vue linguale. Les affinités phylogénétiques de ces poissons acanthodiens sont discutées, ainsi que leur signification paléoenvironnementale.

MOTS CLÉS
acanthodien, Dévonien, Spitsberg, systématique, *Mesacanthus*, *Xylacanthus*.

ABSTRACT
Two new acanthodian species are described from the Spitsbergen Old Red Sandstone. *Mesacanthus grandis* n.sp. is represented by an articulated specimen showing unornamented body scales, elongate modified tectal scales, and a mesacanthid type of scapula. The second species, *Xylacanthus minutus* n.sp. is represented by a right branch of the mandible in lingual view, showing a single row of triangular striated teeth with an anterior flange. Phylogenetic affinities of these forms are discussed as well as their paleoenvironmental significance.

KEY WORDS
acanthodian, Devonian, Spitsberg, systematics, *Mesacanthus*, *Xylacanthus*.

INTRODUCTION

Matériel et méthodes

Le matériel consiste en deux spécimens de poissons acanthodiens. Le premier est articulé et fossilisé dorso-ventralement, le second est formé d'une hémi-mandibule droite.

La gangue ne réagissant pas à l'acide formique ou acétique, le spécimen articulé a été préparé mécaniquement par l'un de nous (D. G.) à l'aiguille montée. L'hémi-mandibule a été dégagée en négatif par dissolution de l'os à l'acide chlorhydrique (P. J.). Le matériel ainsi préparé a ensuite été étudié à partir d'un moulage en élastomère.

La figuration a été essentiellement réalisée à la chambre claire. Le spécimen articulé était placé sous immersion dans une eau contenant de l'alcool pour les prises de vues photographiques, et les reliefs de l'hémi-mandibule ont été accentués par pulvérisation à la fumée de magnésium (oxyde de magnésium).

Localisation géographique

Lors de l'expédition au Spitsberg de 1969, organisée par le CNRS et le Muséum national d'Histoire naturelle de Paris, de nombreux vertébrés dévoniens ont été récoltés. Parmi eux, beaucoup d'acanthodiens furent découverts, dont les deux formes décrites ici.

Ces spécimens proviennent de deux localités de la rive est, au fond du Woodfjord. Elles sont situées de part et d'autre de Woodfjorddalen, la première sur le versant nord-est du mont Wagner et la seconde sur le versant sud-sud-ouest du mont Nidhogg (Fig. 1A, B).

Géologie

Les sédiments dévoniens de cette région sont dominés par le faciès Vieux Grès Rouges semblable à celui des roches plus ou moins contemporaines de Grande-Bretagne ou de Podolie. Ce faciès est caractérisé par la prédominance des sédiments arénacés détritiques plus ou moins grossiers dont la couleur varie du rouge brique au gris-vert (Goujet 1984).

Les affleurements fossilifères font partie de la Formation de Wood Bay (Dévonien inférieur). Le matériel du mont Nidhogg, comme celui du mont Wagner, appartient à la division faunique

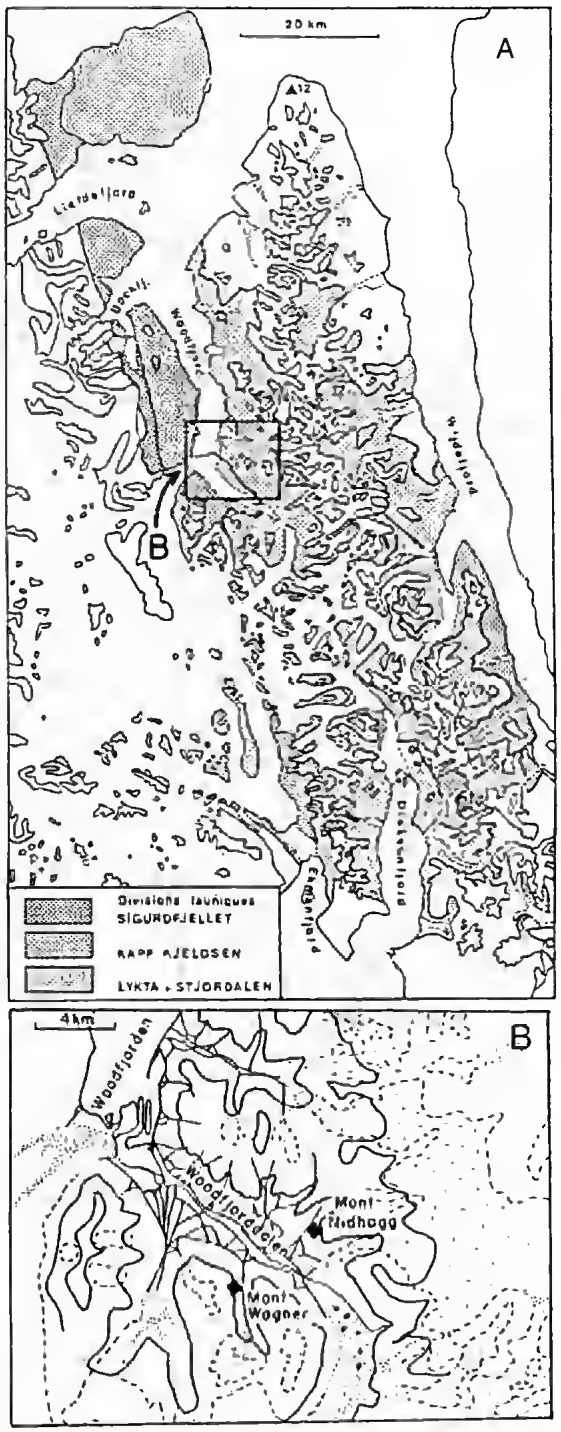

Fig. 1. — Carte des affleurements de la formation de Wood Bay au nord du Spitsberg. **A**, vue générale avec les trois divisions fauniques principales, extrait de Goujet 1984a (modifié de Friend Moody-Stuart 1972); **B**, localisation géographique. Échelle : 20 km.

de Lykta (Fig. 1A ; Goujet 1984 : 26, fig. 2).
Outre sa richesse en vertébrés fossiles, la découverte, dans la Formation de Wood Bay, de traces de trilobites (*Cruziana* et *Rusophycus*) et de *Lingula* remet en doute les conclusions sédimentologiques de plusieurs auteurs concernant la Formation de Wood Bay. Il ressort de l'analyse sur le paléomilieu de cette formation par Goujet (1984 : 32) et Goujet & Emig (1985 : 945) qu'elle correspondrait à un milieu marin côtier, sub-tidal.

SYSTÉMATIQUE

Classe ACANTHODII Owen, 1846
Ordre ICHNACANTHIFORMES Berg, 1940
Famille ICHNACANTHIDAE Woodward, 1891
Genre *Xylacanthus* Ørvig, 1967

Xylacanthus minutus n.sp.
(Fig. 2)

HOLOTYPE. — Le seul matériel de ce nouvel Ischnacanthidae est un os dentigère portant six dents. MNHN P SVD 247 est l'holotype de *Xylacanthus minutus* n.sp. Il représente une hémi-mandibule droite, en vue linguale. Ce spécimen fut récolté lors de la dernière expédition CNRS-Muséum en 1969 au Spitsberg.

NIVEAU-TYPE. — Formation de Wood Bay (Division faunique de Lykta), Lochkovien sup. (Siegenien).

LOCALITÉ-TYPE. — Talus, flanc NE de Wagnerfjellet, Andrée Land, Vestspitsbergen, Svalbard (Fig. 1A).

ÉTYMOLOGIE. — Le nom spécifique, *minutus*, est donné en raison de la taille (86 mm) de la mandibule de cette nouvelle espèce, beaucoup plus petite que celle de l'autre espèce du genre (350 mm).

DIAGNOSE. — *Xylacanthus minutus* est un Ischnacanthiformes possédant un os dentigère à une seule rangée de dents. Les dents sont réunies, le long de la bordure labiale de la lame dentigère, par une crête portant de quatre à cinq denticules réguliers. Les dents portent de trois à cinq crêtes aiguës sur leur face médiale, séparées par de profondes cannelures. Elles sont aplaties, presque triangulaires en section parabasale. Le champ médial de la mâchoire est pourvu de petits tubercules sur sa moitié proximale.
La forme de l'os dentigère, les striations marquées des dents, la forme des denticules portés par la crête entre les dents principales, et la forme du processus postérodorsal de la région articulaire permettent d'attribuer ce spécimen au genre *Xylacanthus*. Il diffère de *Xylacanthus grandis* par sa petite taille, par la forme, latéralement comprimée, de ses dents et par la morphologie de la crête labiale.

DESCRIPTION ET REMARQUES
La mandibule n'est représentée que par son os dentigère, qui mesure 86 mm de longueur. La transposition, à partir de cet os, des proportions d'*Ischnacanthus gracilis*, dont on possède des spécimens en connection, permet d'estimer que l'individu complet devait mesurer plus de 50 cm de long.
L'os dentigère est étroit et haut postérieurement. Sa forme générale rappelle celle de *Xylacanthus grandis* (Ørvig 1967b). L'ossification des champs dentaires (os dentigère) est peu importante, contrairement à celle de *Gomphonchus* (Gross 1957) ou d'*Acanthodopsis*.
L'os dentigère possède une rangée de six dents principales, aplaties latéralement (presque triangulaires en section parabasale) et courbées médialement, comme celles d'*Atopacanthus* (Ørvig 1957), d'*Acanthodopsis* (Miles 1966) et de l'*Ischnacanthida* indet. de Séripona (Gagnier *et al.* 1988). Les dents sont élancées et portent trois à cinq crêtes verticales sur leur face médiale. Une ou deux petites cuspides apparaissent à la base de ces crêtes. Les dents sont reliées par une longue crête portant de quatre à cinq petits denticules entre les cuspides principaux. Ørvig (1967a, pl. 2, fig. 3) figure une structure similaire chez *Xylacanthus grandis*. Il y décrit également une rangée de quatre à cinq denticules formant une crête entre les dents.
Sur la face linguale, à la base des dents, un sillon antéro-postérieur, bordé d'un champ dentaire secondaire, s'élargit antérieurement comme chez la majorité des Ischnacanthidae, sauf *Ischnacanthus* et l'*Ischnacanthida* indet. de Séripona (Gagnier *et al.* 1988). Ce champ dentaire (lingual) n'est que peu marqué. Bien qu'il porte des dents ou des tubercules dans la majorité des espèces, il est lisse chez *Atopacanthus* ou *Persacanthus* par exemple. *Xylacanthus minutus* n.sp. montre une situation intermédiaire puisqu'il ne porte de petits tubercules que sur la moitié postérieure (proximale), comme chez l'Ischnacanthiformes indet. d'Iran (Blieck *et al.* 1980) et, de façon plus développée, chez *Xylacanthus grandis*.

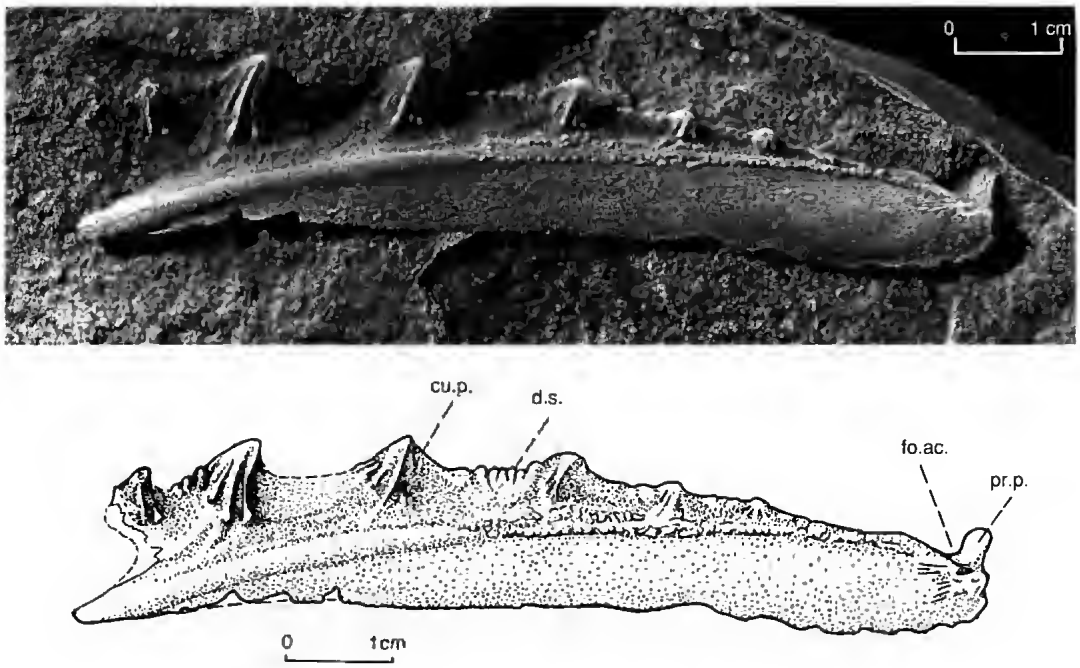

FIG. 2. — *Xylacanthus minutus* n.sp., mont Wagner, Spitsberg, MNHN P SVD 247 : fragment dentifère de mandibule droite en vue linguale. **cu.p.**, cuspide principal ; **d.s.**, denticule secondaire ; **fo.ac.**, fossette accessoire ; **pr.p.**, processus postéro-dorsal. Échelle : 1 cm.

La région articulaire de l'os dentigère possède un processus bordant postérieurement une encoche dorsale qui correspond à une fossette accessoire, mais pas à l'articulation principale de la mandibule. Elle est entourée par un petit bourrelet comme chez *Taemasacanthus* (Long 1986). Le processus est élevé dorsalement comme celui de *Xylacanthus grandis*. La fosse articulaire proprement dite était en position latérale par rapport à ce processus qui marque le côté lingual.
Le processus postérieur de l'os dentigère se projette latéralement. Sa cavité postérieure, « en cuillère », correspondait à la limite antérieure de la zone articulaire de la mandibule.

Ordre ACANTHODIFORMES Berg, 1940
Famille MESACANTHIDAE Moy-Thomas, 1939
Genre *Mesacanthus* Traquair, 1888

Mesacanthus grandis n.sp.
(Figs 3, 4)

HOLOTYPE. — Le seul spécimen d'acanthodien articulé connu de la série des Vieux Grès Rouges du Spitsberg, MNHN P SVD 246, est l'holotype de *Mesacanthus grandis* n.sp. Il est conservé en vue dorsale partielle, la tête, incomplète, est courbée suivant un angle de 90° environ par rapport à l'axe du corps. Une partie de la ceinture pectorale, l'aiguillon dorsal et la nageoire caudale sont visibles.
Initialement, la couverture écailleuse était transparente à l'observation sous liquide. Pour la préparation et l'étude, le spécimen a été coloré à l'alizarine et préparé manuellement. Cette préparation a nécessité plus de sept mois de travail (D. G.).

NIVEAU-TYPE. — Formation de Wood Bay (division faunique de Lykta), Lochkovien supérieur (Siegenien).

LOCALITÉ-TYPE. — Talus, flanc nord de Nidhogg dans une vallée à l'est de Woodfjorddalen (Fig. 1A).

ÉTYMOLOGIE. — Le nom spécifique signifie que cette nouvelle espèce est très grande pour le genre.

DIAGNOSE. — Acanthodiforme, atteignant plus de 10 cm de longueur et dont le rapport de la hauteur estimée sur la longueur totale est d'environ 0,11. Les écailles du corps sont de forme rhombique, plates et sans ornementation. La tête est couverte de tessères allongées disposées dans le plan longitudinal.

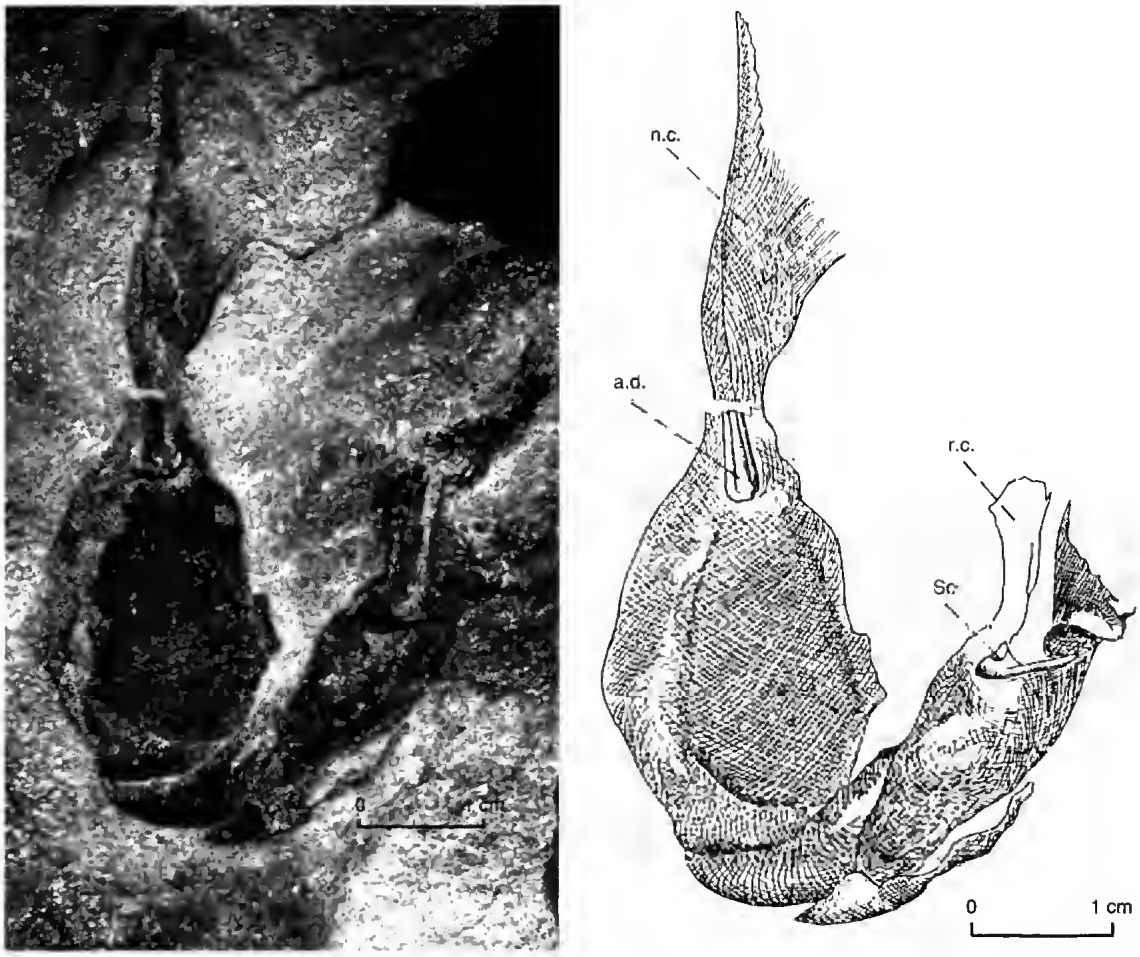

FIG. 3. — *Mesacanthus grandis* n.sp., mont Nidhogg, Spitsberg, MNHN P SVD 246. **a.d.**, aiguillon dorsal ; **n.c.**, nageoire caudale ; **r.c.**, région céphalique ; **Sc**, Scapula. Échelle : 1 cm.

Ce spécimen est attribué aux Acanthodiformes par la présence d'une seule nageoire dorsale et par la forme des écailles à base mince et couronne lisse et plate, aux Mesacanthidae par la présence d'un aiguillon dorsal superficiellement inséré dans le corps.
Il est attribué au genre *Mesacanthus* et non à *Triazeugacanthus* du fait de la dimension réduite des écailles et par la présence de tessères oblongues sur le sommet de la tête. Ce spécimen diffère de *Mesacanthus mitchelli* par sa grande taille, la position postérieure de sa nageoire dorsale et la présence d'un seul sillon latéral sur l'aiguillon dorsal.

DESCRIPTION ET REMARQUES

Mesacanthus grandis n.sp. (Fig. 3) est un acanthodien de forme très allongée. Le rapport estimé de la hauteur sur la longueur totale du corps est d'environ 0,11 alors qu'il est de 0,14 pour les Mesacanthidae, *Mesacanthus* et *Triazeugacanthus*. Compte tenu du mode de présentation du fossile, cette différence n'exclut pas une erreur d'évaluation de la longueur du spécimen redressé. On peut estimer que la longueur de la tête (du museau à la scapula) occupait une partie importante de l'animal (0,18) comme chez *Mesacanthus mitchelli*.

Nageoire

La nageoire dorsale est nettement postérieure, étant donné la forme de la caudale, notamment le développement de son lobe ventral. La nageoire anale, non visible sur le fossile, devait probable-

ment être franchement antérieure par rapport à la dorsale. La nageoire caudale est courte, avec un lobe hypochordal bien développé.
Le fragment du tégument correspondant à la région dorsale de la tête comprend des tessères allongées. Ces tessères se raccourcissent et se confondent avec les écailles du corps en arrière de la position présumée de la chambre branchiale. Les tessères semblent s'organiser en rangées longitudinales dans la région antérieure, un arrangement particulier semblable à celui de *Mesacanthus mitchelli* d'après les remarques de Watson (1937 : 75). Les écailles de la tête et du corps ne sont pas ornementées.

Écailles
Les écailles sont petites (0,4 mm), lisses, rhombiques et ne semblent pas imbriquées. Elles sont proportionnellement plus petites que celles du genre *Triazeugacanthus* et rappellent, par leurs proportions, celles de *Mesacanthus mitchelli*. De taille uniforme sur le tronc, elles sont plus petites antérieurement. Elles sont alignées en rangées obliques sur les flancs. Au niveau de la nageoire caudale, elles recouvrent le voile. En forme de petits rectangles, elles vont en se réduisant vers le bord distal, formant des rangées parallèles au bord d'attaque, perpendiculaires à l'axe du corps. Sur les fragments de tégument de la région de la tête, on repère une série d'éléments écailleux allongés qui correspondaient vraisemblablement à des tessères. Compte tenu de leurs dimensions et de leur type de conservation, il n'a pas été possible de les figurer : elles sont en effet partiellement transparentes et ne réagissent que partiellement à la coloration par l'alizarine, aussi le contour de ces éléments qui demeure en partie flou ne peut-il être tracé avec une précision suffisante.

Ceinture scapulaire
La ceinture scapulaire de *Mesacanthus grandis* n.sp. n'est représentée que par sa scapula (Fig. 4). Cet élément est formé d'une ossification périchondrale, qui comprend une tige dorsale s'évasant vers le bas en une expansion triangulaire. En largeur, cette base correspond environ au tiers de la hauteur de la tige scapulaire. La base de la scapula possède, comme celle de *Triazeugacanthus*

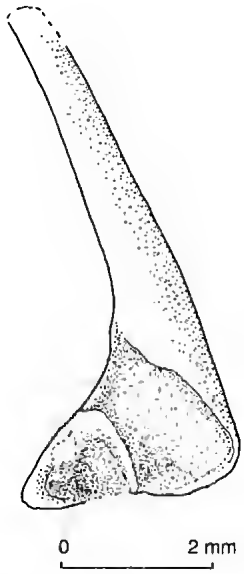

FIG. 4. — *Mesacanthus grandis* n.sp., mont Nidhogg, Spitsberg, MNHN P SVD 246 : scapula droite en vue mésiale. Échelle : 2 mm.

affinis, une fosse glénoïde très marquée (Fig. 4), mais qui semble proportionnellement plus petite que chez ce dernier. Cette fosse glénoïde se situe sur la face postérieure de la lame latérale. Une seconde petite lame, probablement postbranchiale, est en continuité avec la tige scapulaire, perpendiculairement à la lame latérale. Elle forme, avec la fosse glénoïde de la lame latérale, une dépression dont la base est mal définie, comme chez tous les exemplaires connus de Mesacanthidae. Il se pourrait néanmoins qu'elle puisse servir de margo radialis. La tige scapulaire est peu élancée comparativement à celle de *Triazeugacanthus affinis* (Miles 1966 : scap, pl. 5-9). Sa forme générale rappelle la scapula de *Mesacanthus mitchelli*, mais dans cette dernière espèce, elle n'a été que succinctement décrite (Miles 1973 : 159, fig. 23).

Aiguillon dorsal
Seule la partie proximale de l'aiguillon dorsal est conservée en place. D'après la forme de la base, il est clair que cet aiguillon n'était pas profondément inséré dans le corps, une caractéristique des Mesacanthidae parmi les Acanthodiformes. Une section transversale ne montre qu'un seul sillon

profondément marqué de chaque côté de l'aiguillon. Il matque l'avant de la nageoire dorsale qui occupait donc une position très postérieure. Le rapport de la distance du museau à l'aiguillon dorsal sur la longueur totale du corps devait être d'environ 0,65, tandis que ce rapport se rapproche de 0,53, tant chez *Triazeugacanthus* que chez *Mesacanthus mitchelli*.

Nageoire caudale

L'axe de la nageoire caudale semble peu relevé. Le lobe hypochordal est petit, triangulaire, et ne s'étend pas jusqu'à l'extrémité de l'axe caudal. Le rapport de la nageoire caudale à la longueur totale du corps est égal à 0,23, tandis qu'il correspond à 0,28 chez *Mesacanthus mitchelli* et à 0,32 chez *Triazeugacanthus affinis*. Le rapport de la hauteur maximale de la nageoire caudale sur sa longueur au pédoncule représente 0,4 chez le *Mesacanthus* du Spitsberg tandis qu'il approche 0,5 chez l'espèce d'Écosse.

CONCLUSIONS

Xylacanthus minutus n.sp. est connu par un os dentigère unique, présentant la morphologie classique des Ischnacanthiformes. Il est mince, élargi pour le support du cartilage de Meckel, et ses dents sont fusionnées. Aucune spirale den-taire n'est connue ; les dents fusionnées sont plus grosses à l'avant. Ceci suggère, comme Ørvig (1973 : 127-130) l'a montré, que de nouvelles dents, sur une nouvelle base, sont périodiquement ajoutées à l'extrémité antérieure de la mâchoire, comme chez les placodermes (voir aussi Valiukevicius 1992 : fig. 5A, pls 1, 4, fig. 3).

L'extrémité postérieure de l'os dentigère chez *Xylacanthus* (Fig. 2) est simple comme chez les Ischnacanthidae *Ischnacanthus*, *Persacanthus*, (Janvier 1977), *Rockycampacanthus* ou *Taemasacanthus* (Long 1986), alors que l'articulation est généralement double chez les Climatiiformes et Acanthodiformes. Un grand processus postéro-dorsal marque l'avant de la région articulaire. Ce processus, en continuité avec la bordure linguale chez *Taemasacanthus*, *Atopacanthus* (Ørvig 1957) et *Persacanthus*, est bien individualisé chez *Xylacanthus*. Chez ce dernier, la fossette accessoire du processus postéro-latéral est basse alors qu'elle est haute chez *Atopacanthus* et *Taemasacanthus*.

Gross (1957) suggère d'utiliser la forme des dents pour séparer les os dentigères de Climatiiformes de ceux des Ischnacanthiformes. Cependant, Denison (1976), après une étude histologique, considère que le seul os dentigère attribué aux Climatiiformes (*Nostolepis* ; Gross 1957 ; Ørvig 1973) se rapporterait au genre *Gomphanchus*, un Ischnacanthiformes. Toutefois, les caractères relevés par Gross restent intéressants ; par exemple, « présence de cuspides secondaires attachées à la cuspide principale », caractère repris par Ørvig (1967a) sous la forme « présence de cuspides secondaires latérales plus nombreuses à l'arrière de la dent ». Chez *Xylacanthus* (Fig. 2), *Persacanthus* et *Taemasacanthus*, une crête postérieure est visible sur chaque dent. La présence de tubercules secondaires ou de crêtes est probablement liée à des types de synchronisation du développement différents pour l'os dentigère et pour le champ morphogénétique des dents.

Un autre caractère présenté par Gross (1957) et qui existe chez la majorité des Ischnacanthifotmes est la présence d'un champ dentigère labial (champ dentigère secondaire). Il est généralement garni de tubercules mais peut être lisse, comme chez *Persacanthus*, ou finement denticulé, comme chez *Xylacanthus*.

La présence de stries sur les dents, leur crête postérieure tuberculée, la largeur du champ lingual très finement denticulé, et la finesse de l'os dentigère du genre *Xylacanthus* permettent d'y voir un intermédiaire morphologique entre *Persacanthus* et le *Nostolepis* de Ørvig (1973). Ce dernier est probablement un Ischnacanthiformes (Denison 1976).

Le spécimen articulé d'acanthodien, *Mesacanthus grandis* n.sp., ne possède qu'une seule nageoire dorsale, caractère distinctif des Acanthodiformes. Ses écailles non ornementées sont également classiques dans cet ordre. L'insertion superficielle de l'aiguillon dorsal, la forme des tessères tectales et la morphologie de la ceinture scapulaire plaident en faveur d'un Mesacanthidae. Toutefois, la présence d'éperons intermédiaires – jusqu'ici considérés comme une exclusivité de la famille au sein des Acanthodiformes – n'a pas été mise en évidence.

Denison (1979 : 47) écrit que le genre *Mesacanthus* correspond à des petits poissons acanthodiens minces et élancés, dont la tête est recouverte d'écailles irrégulières, et qui peuvent posséder de larges plaques inter-orbitaires. Chez *Triazeugacanthus* (Miles 1966 ; Gagnier 1996), la tête est couverte d'écailles régulières et représente probablement un stade primitif à partir duquel la tendance à la formation des plaques inter-orbitaires a pu évoluer. La forme allongée des tessères tectales est un caractère partagé entre *Mesacanthus mitchelli* et *M. grandis* n.sp.
Toutefois, les tessères tectales existent chez tous les Climatiiformes, sauf *Euthacanthus*. Watson (1937), Novitskaya & Obruchev (1964 : 272) et Miles (1965 : 247 ; Miles *in* Moy-Thomas & Miles 1971 : 74) considèrent que l'évolution des acanthodiens mène à une réduction du squelette dermique. La présence de tessères chez les Climatiiformes serait donc primitive. Miles (1971) interprète les plaques inter-orbitaires de *Mesacanthus* ou encore l'os nasal de *Triazeugacanthus affinis* comme des stades régressifs secondaires. En revanche, Denison (1979 : 5) fait remarquer que les Climatiiformes considérés comme les moins évolués ont des tessères plus petites ou des écailles peu modifiées (cf. *Euthacanthus*). De plus, les tessères tectales des Climatiiformes sont en général des écailles modifiées, élargies, qui partagent une base commune. Nous partageons l'opinion de Denison qui considère deux voies possibles de spécialisation au sein des acanthodiens. Une première voie se traduirait par l'élargissement des formations osseuses ; la seconde, par la diminution de l'écaillure chez certains Acanthodidae tels que *Traquairichthys* et *Acanthodes*. Il s'agirait alors d'une régression secondaire.

La scapula de *Mesacanthus*, comme celle de *Triazeugacanthus*, possède une haute tige dorsale (Fig. 4). Cette tige est circulaire ou ovale en section comme celle des autres acanthodiens. Chez *Mesacanthus grandis* n.sp., la base de la scapula semble s'étendre ventralement, couvrant la partie latérale de l'aiguillon pectoral (Fig. 4). Chez *Triazeugacanthus affinis*, la base de la scapula est petite et ne couvre probablement pas la partie latérale de l'aiguillon. Il semble toutefois exister une concavité pour la réception de ce dernier et une autre pour l'articulation d'un procoracoïde. Cependant, aucune trace de cette ossification n'est visible.
Bien que la scapula des Mesacanthidae reste assez mal connue, elle montre des caractères qui lui sont propres, tels que la présence d'une tige dorsale (supra-scapulaire) très haute et une fosse postéro-médiale associée à la lame latérale plutôt qu'à la tige dorsale comme c'est le cas chez les autres acanthodiens. Contrairement aux Cheiracanthidae, la scapula des Mesacanthidae posséderait une portion basale qui enserrait l'aiguillon.
Dans les Vieux Grès Rouges de la Formation de Wood Bay, les acanthodiens apparaissent comme des raretés comparées aux placodermes, aux agnathes ou aux porolepiformes. En fait, on les rencontre en abondance dans les niveaux de base de la formation (division faunique de Sigurdfjellet) où d'emblée ils sont représentés par de grandes formes, puisque des aiguillons de l'ordre de 10 cm de long ne sont pas rares. Plus haut dans la série, leurs restes sont plus clairsemés. La découverte d'un individu complet de *Mesacanthus* atteste cependant qu'ils vivaient à proximité du lieu de leur découverte ou dans la tranche d'eau immédiatement sus-jacente. La nature du sédiment témoigne d'un environnement momentanément turbide probablement lié à une décharge sédimentaire soudaine et brutale. On notera que *Mesacanthus grandis* a été découvert dans les niveaux supérieurs de la Formation de Wood Bay et que, plus haut dans la série stratigraphique, les influences marines évidentes s'accompagnent d'accumulations d'écailles parmi lesquelles celles d'acanthodiens sont les plus abondantes. En conclusion, contrairement à ce que pourrait faire croire une première impression, les acanthodiens, prédateurs actifs à cette époque, seraient ici des indicateurs d'influences marines plutôt que des témoins de l'apport d'eau douce. Il est probable qu'une incursion à proximité des côtes leur fut accidentellement fatale et qu'ils y trouvèrent le lieu de leur ensevelissement.

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Ptyctodontid fishes (Vertebrata, Placodermi) from the Late Devonian Gogo Formation, Western Australia, with a revision of the European genus *Ctenurella* Ørvig, 1960

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Long J. A. 1997. — Ptyctodontid fishes (Vertebrata, Placodermi) from the Late Devonian Gogo Formation, Western Australia, with a revision of the European genus *Ctenurella* Ørvig, 1960. *Geodiversitas* 19 (3) : 515-555.

ABSTRACT

A new, almost complete specimen of the ptyctodontid placoderm *Campbellodus decipiens* Miles *et* Young, 1977 enables description of the skull roof, trunk shield, visceral skeleton, pelvic girdle, dermal scale cover, and parts of the vertebral column. A new reconstruction of the head shield of *Ctenurella gladbachensis* Ørvig, 1960 from Bergisch-Gladbach permits this taxon to be generically defined from the Gogo species previously referred to that genus. The Gogo form is here referred to *Austroptyctodus* n.g. A new specimen of *Austroptyctodus gardineri* Miles *et* Young, 1977, together with new observations of *Chelyophorus verneuili* Agassiz, 1844 and *Ctenurella gladbachensis* Ørvig, 1960, shows new information for the endocranium, the hyoid arch and visceral skeleton, identifying the previously identified "metapterygoid" elements as paired nasal bones. The large visceral skeleton bone posterior to the jaw joint in ptyctodontids is here identified as an elongated interhyal.

KEY WORDS
Ptyctodontida, Devonian, Placodermi, Gogo, Australia, *Austroptyctodus* n.g., *Ctenurella*, *Chelyophorus*.

RÉSUMÉ

Une nouvelle description du toit crânien, de la cuirasse thoracique, du squelette viscéral, de la ceinture pelvienne, de l'écaillure et de quelques éléments de la colonne vertébrale est proposée à partir d'un nouveau spécimen subcomplet du ptyctodonte *Campbellodus decipiens* Miles *et* Young, 1977. Une nouvelle reconstitution du toit crânien de *Ctenurella gladbachensis* Ørvig, 1960 (Frasnien de Bergish-Gladbach, Allemagne) permet de redéfinir le genre *Ctenurella*, en y incluant les formes de Gogo qui y sont rapportées. Un nouveau genre *Austroptyctodus* est créé. À partir du matériel qui définit *Austroptyctodus gardineri*, espèce-type du genre, et d'une révision de *Chelyophorus verneuilli* Agassiz, 1844 et de *Ctenurella galdbachensis*, de nouvelles informations sur l'endocrâne, l'arc hyoïde et le squelette viscéral des ptyctodontes sont fournies. Ainsi le « métapterygoïde » est interprété comme des os nasaux paits, de même l'os du squelette viscéral situé en arrière de l'articulation de la mandibule serait un interhyal de forme allongée.

MOTS CLÉS
Ptyctodontida, Devonien, Placodermi, Gogo, Australie, *Austroptyctodus* n.g., *Ctenurella*, *Chelyophorus*.

INTRODUCTION

The ptyctodontid placoderms have for many years been a problematic and poorly-known group of extinct fishes. Early workers identified ptyctodontids only from their characteristic tooth plates and thus allied them to the holocephalans (Pander 1858; Woodward 1891), although when the exoskeletal trunk armour was described by Jaekel (1907) he compared it favourably with the sturgeon *Acipenser*, an osteichthyan fish. Both Dollo (1907) and Goodrich (1909) rejected this view and argued that they were placoderm fishes. Watson (1934) described more complete material of a new form he called *Rhamphodopsis* and further characterised them as placoderm fishes, and this view was strengthened by further discoveries of well-preserved specimens (Watson 1938). Major discoveries of complete, well-preserved ptyctodontids from the Bergisch-Gladbach region of Germany described by Ørvig (1960, 1962, 1971, 1980) led him to revive the earlier hypothesis of a holocephalan affinity between ptyctodontids and holocephalans, proposing them to be ancestral to the holocephalans, an opinion followed by Stensiö (1963, 1969) and Jarvik (1980). However, many researchers working with placoderm fishes or chondrichthyans opposed this view, regarding ptyctodontids as placoderm fishes (*e.g.* Patterson 1965; Stahl 1967; Miles 1967; Miles & Young 1977; Denison 1978; Forey & Gardiner 1986; Young 1986). Today this view is widely held, and the placoderm affinity of ptyctodontids has been borne out by several recent computer analyses of placoderm interrelationships (*e.g.* Forey & Gardiner 1986; Carr 1991, 1995; Goujet & Young 1995).

The problematic position of the group within the Placodermi has been raised. They have been proposed as a primitive sister group to other placoderms (Miles & Young 1977; Young 1980), as a primitive group more derived than acanthothoracids plus rhenanids, but plesiomorphic to all other placoderms (Forey & Gardiner 1986), or as a sister taxon to the petalichthyids (Goujet 1984; Goujet & Young 1995; Carr 1995).

Most of the known ptyctodontid taxa (some forty-seven species, Carr 1995, amended) are based solely on tooth-plates (Denison 1978), although the following species have been described from relatively complete, well-preserved material of head and trunk armour: *Ctenurella gladbachensis* (Ørvig 1960, 1971), *Austroptyctodus gardineri* n.g. (Miles & Young 1977, here erected as a new genus), *Rhamphodopsis threiplandi* and *R. trispinatus* (Watson 1934, 1938; Miles 1967), *Rhynchodus tetrodon* (Newberry 1873; Jaekel 1903; Gross 1933; Stensiö 1959 ; Miles 1967), *Chelyophorus vernueili* (Agassiz 1844; Eichwald 1859; Obrucheva 1983), and *Ptyctodopsis menzeli* (Denison 1985). Recent new discoveries of other relatively complete ptyctodontids have been made in North America from the Frasnian Mt. Elden site in Arizona (Johnson & Elliott, in press) and from the Pinicon Range Formation, Iowa (Hickerson 1993; work in prep.).

The superb three-dimensionally preserved material of ptyctodontids from the Frasnian Gogo Formation of Western Australia has provided the most detailed knowledge of the group to date. Miles & Young (1977) described several specimens of a new species they assigned to the genus *Ctenurella* Ørvig, 1960. Two incomplete specimens were placed in the new genus and species, *Campbellodus decipiens*. Further observations on the structure of the Gogo "*Ctenurella*" were described by Gardiner (1984a) and Forey & Gardiner (1986). New finds of Gogo fishes made during expeditions in 1986-1989 by the author include many new arthrodires (Long 1987, 1988a, 1988b, 1990b, 1994a, 1995b) as well as two nearly complete, articulated specimens of ptyctodontids, which belong to the previously described taxa.

The aim of this paper was originally to describe this new material of the Gogo ptyctodontids in detail, by comparison with other specimens of ptyctodontids, made available for the author to study at the Muséum national d'Histoire naturelle. The well-preserved nature of the Gogo specimens has permitted new further interpretations of the structure of these other taxa. Comparisons with the Bergisch-Gladbach *Ctenurella* indicated that its skull roof and visceral skeleton could be reinterpreted. It soon became apparent that this species differs in several major features from the Gogo species, and thus a new genus, *Austroptyctodus* n.g., is here erected for the Gogo species.

DERMAL BONE TERMINOLOGY IN PTYCTODONTIDS

The central median bone that bears the X-shaped confluence of the two main dorsal sensory-line canals has been previously called the centro-nuchal (Ørvig 1960), the centro-median (Miles 1967), the nuchal (*e.g.* Miles & Young 1977; Long 1988a) or the postpineal (Denison 1978, 1985; Johnson & Elliott 1996). Confusion over the name of this bone has arisen, largely due to the supposed presence of a small posterior median element in *Rhamphodopsis* which was termed the nuchal. Examination of specimens of *Rhamphodopsis threiplandi* in the collections of the Natural History Museum, London, and in the Field Museum, Chicago, shows that the posterior nuchal element is not present in this genus, but was misinterpreted by Watson due to the crushed and fractured nature of the Edderton specimens. The area of exposed bone immediately behind the paired central plates is most likely the crushed occipital ossifications of the braincase, as this region lacks any trace of dermal ornamentation on the Edderton specimens.

In other placoderm groups that have the supraorbital sensory line canals as well as posterior pit-line canals converging mesially onto one median bone, as in ptyctodontids, this bone is generally identified as the nuchal, especially so when it extends all the way to the posterior margin of the skull roof (*e.g.* as in petalichthyids; Woodward 1941; Gross 1963; Young 1985; Liu 1992). This condition is also seen in the primitive arthrodire-like form *Wuttagoonaspis* (Ritchie 1973) and in phyllolepids, where the nuchal plate is broad rather than elongate, but still bears the confluence of several sensory-line canals (Long 1984b). In many primitive arthrodires this bone has a similar elongate shape and also has similar contact relationships with neighbouring paranuchal, central, and postorbital or preorbital bones, although the convergence of the sensory-line canals is lacking.

Thus the median canal-bearing bone in ptyctodontids is interpreted here as homologous to the nuchal of other primitive placoderms, rather then a postpineal as this element, where present in some placoderm groups, is always a median bone lacking sensory-line canals (*e.g.* as in antiarchs, Denison 1978), or maybe represented by a series of irregularly-shaped anamestic bones (as in the rhenanid *Asterosteus*, Stensiö 1969, fig 92). For the other bones in the head shield and cheek of ptyctodontids, papers published since Miles & Young (1977) use a consistant terminology. However, the large paired ventral bones in the trunk shield that have been called either the anterior ventrolaterals (Gross 1933; Miles 1967) or the interolaterals (Watson 1938; Denison 1978, 1985) require discussion. Ørvig (1960) regarded them as a combination of both elements and termed them the interolateral-anterior ventrolaterals. The anterior ventrolateral plates in primitive placoderms, such as petalichthyids (*Lunaspis*, Gross 1961), early arthrodires (actinolepids, phlyctaenaspids, Goujet 1984b), phyllolepids (Long 1984b) and *Wuttagoonaspis* (Ritchie 1973) are named so because there is also a posterior ventrolateral plate present posterior to them. All of these forms also bear paired interolateral plates forming the anterior ventral margin of the shield and meeting the spinal plates dorsally, and in all cases having an expanded anteriorly-facing postbranchial lamina with rows of triangular tubercles. In acanthothoracids (e.g. *Romundina*, Ørvig 1975) and rhenanids (e.g. *Jagorina*, Stensiö 1969) there is only one pair of large ventral plates and these also form the anterior margin of the ventral lamina of the trunk shield and have a postbranchial lamina which in life presumably formed the posterior wall of the branchial chamber. However, it is known that the position of the scapulocoracoid in arthrodires generally sits between the anterior lateral, the spinal and the anterior ventrolateral plates (and also between the interolateral in *Dicksonosteus*, Goujet 1984b). Similarly, in antiarchs, it lies within the bounds of the anterior ventrolaterals, even though only remnants of it have been found in primitive forms (e.g. *Procondylolepis*, Young & Zhang 1992). Thus its condition in ptyctodontids would imply that the interolateral has expanded ventrally to include the scapulocoracoid, or that it has indeed fused with the anterior ventrolateral to be a compound bone (as suggested by Ørvig 1960, also Stensiö 1959). The identifi-

cation of the bones in ptyctodontids comes down to the overall shape in that they are narrow bones without posteriorly extended ventral laminae, bordering, in the trunk shield, the anterior ventral margin of the trunk and contacting the spinal plate dorsally, and the fact that they bear the well-developed postbranchial lamina with rows of triangular tubercles, a feature never found in any placoderm anterior ventrolateral plate (because interolaterals are also present in the same armour). Thus it is here suggested that they represent interolateral plates. This hypothesis implies that the ptyctodontid trunk shield is more specialised than those of other placoderms in the secondary loss of both anterior and posterior ventrolaterals. In this respect they could parallel the evolution of phyllolepids, now regarded as derived arthrodires in the loss of posterior dorsolateral plates and the fusion of upper jaw elements (based on materials of a new phyllo-lepid from New South Wales under study by Dr. A. Ritchie, pers comm. 1995).

MATERIALS AND METHODS

The ptyctodontids from Gogo were prepared by the standard acetic acid technique using about 5-10% concentration, strengthened with dilute B30 Mowital in acetone solution (from Hoescht). The delicate nature of the *Austroptyctodus* specimen called for epoxy resin transfer preparation. Before embedding the specimen in resin, a latex peel of the exposed surface derail was made. All photographs are of specimens whitened with ammonium chloride, except for the Bergisch Gladbach specimens which were photographed under alcohol.

The new Gogo specimens were compared with the following ptyctodontid material. These results will form the basis of a future revision of the Euramerican ptyctodontids:

– *Austroptyctodus gardineri* n.g. (Miles *et* Young, 1977). All specimens held in the Natural History Museum, London. Upper Devonian (Frasnian), Gogo Formation, Western Australia.

– *Chelyophorus verneuili* Agassiz, 1844. Original Agassiz collection held in the Palaeontological collections of the Muséum national d'Histoire naturelle, Paris. Upper Devonian (Fammenian), Dankov-Lebedyan beds, USSR.

– *Ctenurella gladbachensis* Ørvig, 1960. Five nearly complete well-preserved specimens held in the Palaeontological collections of the Muséum national d'Histoire naturelle, Paris; other specimens in the Natural History Museum, London. Middle-Upper Devonian (Upper Givetain/Lower Frasnian), Oberer Plattenkalk, Germany.

– *Ptyctodopsis menzelli* Denison, 1985. Type specimen held (on display) in the County Museum, Iowa City, Iowa; additional specimens held in the Geology Department collection, University of Iowa, Iowa City. Middle Devonian (Upper Givetian), Cedar Valley Limestone, USA.

– *Rhamphodopsis threiplandi* Watson, 1934. Specimens in the Field Museum, Chicago and in the Natural History Museum, London. Middle Devonian (Eifelian), Middle Old Red Sandstone, UK.

– *Rhynchodus tetrodon*. Cast of the holotype held in the Natural History Museum, London. Upper Devonian (Frasnian), Kellwasserkalk, Germany.

– Specimens of an undescribed new genus of ptyctodontid from the Spring Grove Member (Givetian), northern Illinois, held by the Geology Department, Augustana College, Rock Island, Illinois.

– Specimens of an undescribed new genus of ptyctodontid from the Gneudna Formation (Upper Givetian-Lower Frasnian), Western Australia, collected by the author and K. Trinajstic in 1995.

All specimens described or cited in this paper are reposited in the palaeontology collections of the following institutions as denoted by these abbreviations:

MNHN	Muséum national d'Histoire naturelle, Paris;
NHM	Natural History Museum, London;
WAM	Western Australian Museum, Perth, Western Australia.

SYSTEMATIC DESCRIPTIONS

Genus *Campbellodus* Miles *et* Young, 1977

TYPE SPECIES. — *Campbellodus decipiens* Miles *et* Young, 1977.

AMENDED DIAGNOSIS. — A moderately large ptyctodontid having a *Ptyctodus*-like crushing dentition with high dorsal process on the upper toothplate; head shield having a breadth/length ratio of 90, the nuchal is subrectangular, almost as broad as long and participates in the posterior margin of the skull-roof, excluding the centrals from mesial contact; submargin-al plate is much deeper posteriorly than anteriorly. Trunk shield with three median dorsal bones, the dorsalmost being a broad, flat spine. Spinal plate very small; anterior median ventral plate more than twice as broad as long. Tail covered with large overlapping scales.

Campbellodus decipiens Miles *et* Young, 1977

Campbellodus decipiens Miles *et* Young, 1977: 145-155, figs 8-14, pls 1, 2A, B, 4A. – Denison 1978: 28. – Long 1987a: 203; 1988a: 443-4, fig. 7; 1988c: 141,143,144, fig. 2B; 1991: 366, 367, fig. 20H; 1995a: 108-110.
Ptyctodus sp. Gardiner *et* Miles, 1975.

"tooth-plates resembling those of *Rhynchodus*" (Brunton, Miles & Rolfe 1969)
"tooth-plates which recall those of *Ptyctodus*" (Miles 1971)

HOLOTYPE. — WAM 70.4.252. This number is not published in the Miles & Young (1977) as the specimen had then been allocated by the provisional British Museum of Natural History number P50905.

OTHER MATERIAL. — NHM P50907, comprising the left spinal plate, left upper toothplate, incomplete left interolateral plate, partial dorsal spine, a dermal scale and parts of perichondral ossifications of the endocranium (Miles & Young 1977). WAM 86.9.672, an almost complete individual, shows the head shield mostly complete, missing only part of the posterior margin on the right side and a small part of the left posterior margin. It shows well the three-dimensional form of the entire articulated trunk shield, the pelvic girdle and endogirdle, body scales and axial skeletal elements. WAM 95.6.112 shows the left upper and lower tooth plates, mirror opposites to those seen in the holotype.

REMARKS. — The new material is regarded as cogeneric with the holotype as the dorsal spine is of the same broad based shape with similar ornamentation, and the isolated preorbital, postorbital and submarginals of the Holotype are all of similar shape and identical proportions in WAM 86.9.672. This genus has been redefined in the light of nearly complete material of the dermal armour, axial skeleton and squamation. Long (1988a) figured a reconstruction of the dermal armour, and commented briefly on its overall morphology, but it is only within the framework of studying the other Gogo ptyctodontid with the comparative material of other European genera that the complete description, and new reconstruction provided here, could be undertaken.

DESCRIPTION

Head shield

The exceptional preservation of WAM 86.9.672 (Figs 1A-C, 2) has enabled the head shield of *Campbellodus* to be restored in its natural three-dimensional form. This is unique for ptyctodontids in which restorations usually show the head shield flattened in dorsal aspect, the one exception being *Ptyctodopsis* (Denison 1985) which is preserved in lateral view. Overall the head shield is 90% as broad as long, being broadest across the postorbital plates posterior to the large orbit. The preorbital plates are exceptionally large, about twice the size of the other skull roof bones, which are approximately the same size as each other. An unusual feature of the skull roof is that the preorbital plates are not in mesial contact with apparently an open pineal notch for the pineal organ. No pineal plate was recovered during the preparation of the specimen, and, as most of the delicate gill arch elements of both sides were found, it is assumed that a pineal plate was either very small (as in *Austroptyctodus* n.g.), or absent. In lateral view, the skull roof shows a slit-like opening at the junction of the postorbital, marginal and submarginal plates, referred to previously by Miles & Young (1977) as the postorbital fenestra and by Long (1988a) as the spiracular slit.

Marginal plate. It was apparently not tightly connected with the lateral margin of the head shield; as its precise dorsal border does not correspond to the well-preserved ventral margin on the lateral face of the head shield, it is presumed to have been loosely attached. The submarginal was probably also free in the skin of the cheek region, but anteriorly contained the opercular cartilage which articulated with the ethmoid ossification of the braincase.

Preorbital plates. (PrO; Figs 1A-C, 2) These are the largest bones of the head, being just over half the total length of the skull. Miles & Young (1977, fig. 8) described and figured one of these plates but wrongly identified it as the right ele-

FIG. 1. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A-C**, head shield; **A**, dorsal view, **B**, ventral view; **C**, right lateral view. **D**, **E**, right marginal plate; **D**, lateral view; **E**, mesial view. **F-H**, median dorsal plates in right lateral view; **F**, median dorsal spine; **G**, median dorsal plate 2; **H**, median dorsal plate 1. **I**, **J**, prepelvic bone and attached endoskeletal pelvic girdle; **I**, ventral view; **J**, dorsal view. **K**, right quadrate in mesial view. All photos whitened with ammonium chloride.

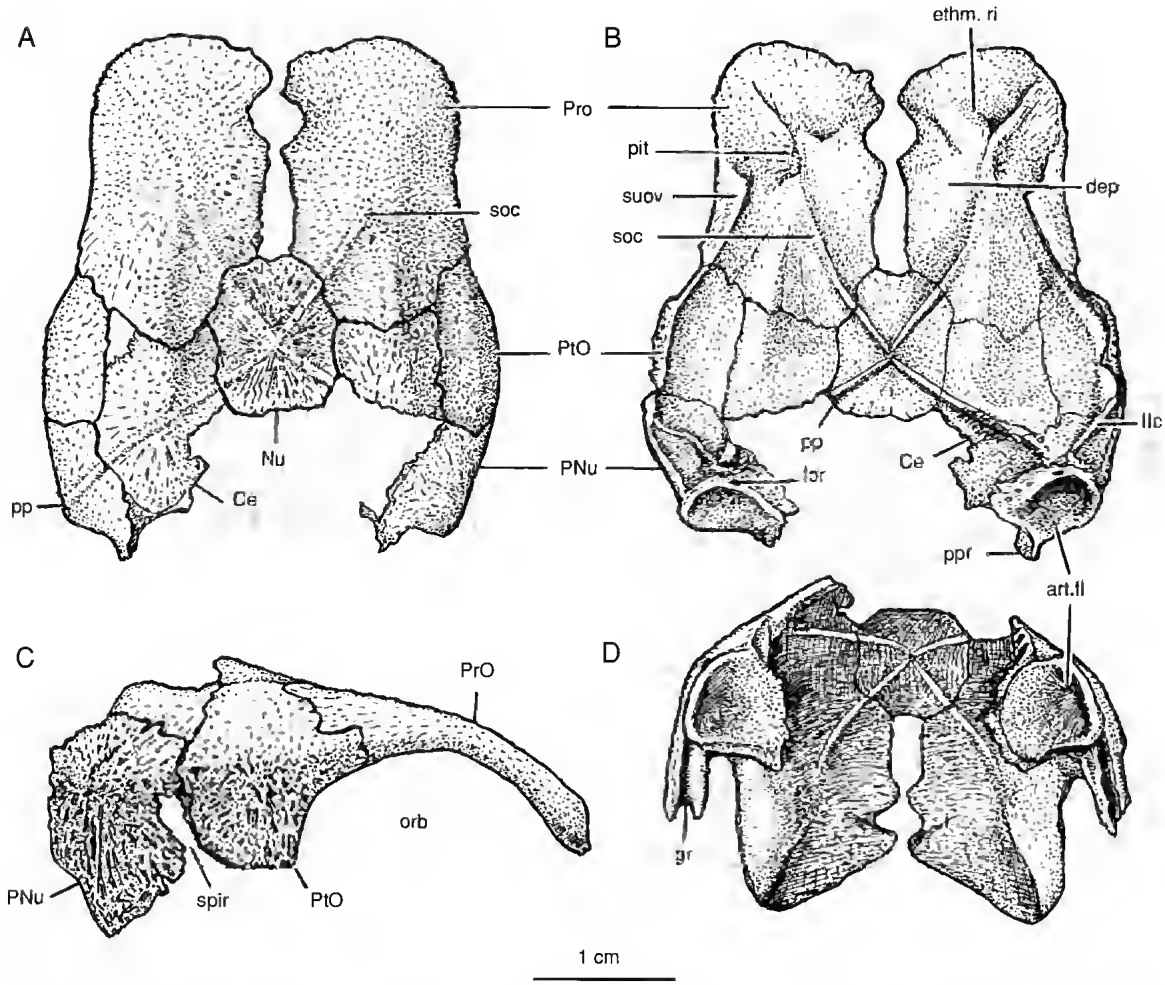

FIG. 2. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A-D**, sketch of head shield; **A**, dorsal view; **B**, ventral view; **C**, right lateral view; **D**, posterior view. **art.fl**, articular flange of neck joint on PNu plate; **Ce**, central plate; **dep**, depression; **ethm.ri**, ethmoid ridge; **for**, foramen; **gr**, groove; **llc**, main lateral line canal; **Nu**, nuchal plate (posterior element); **orb**, orbit or orbital margin; **P**, pineal plate or space provided for it in the head shield; **pit**, pit for insertion of eye muscles; **PNu**, paranuchal plate; **pp**, posterior sensory-line canal on head shield; **ppr**, posterior process of PNu plate; **PrO**, preorbital plate; **PtO**, postorbital plate; **soc**, supraorbital sensory-line canal; **spir**, spiracular slit; **suov**, supraorbital vault.

ment when in fact it is the left preorbital plate, as verified by direct comparison with the articulated head shield of WAM 86.9.672. The preorbital plates are subrectangular in form, having a breadth/length index of between 56-60, for both specimens. They show a weakly concave lateral margin, gently convex anterior margin, strongly convex posterior margin, and gently concave mesial margins with a well-defined anterior notch for the pineal foramen. In lateral view (Figs 1C, 2C), the preorbital plates are weakly curved, flexing over the mid-point of the orbit. The path of the supraorbital sensory-line canal is only visible in dorsal view in the posterior part of the plate, faintly seen mainly through a single row of minute pores opening from within the spaces of the reticulate ornamentation. In visceral view, the tubular sensory-line canals are clearly seen (Fig. 2B, soc, pp, llc), disappearing within the centre of the bone at the ossification centre of the plate. The main lateral line sensory-line canal that comes off the marginal plate enters the

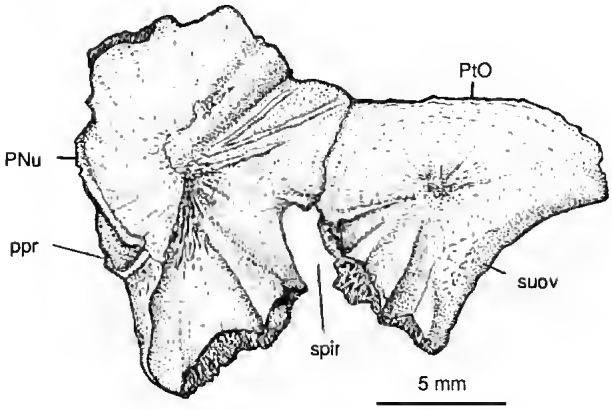

FIG. 3. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. Left paranuchal and postorbital plates in mesial view, showing spiracular slit. **PNu**, paranuchal plate; **ppr**, posterior process of PNu plate; **PtO**, postorbital plate; **spir**, spiracular slit; **suov**, supraorbital vault.

preorbital at its posteroventral corner and runs directly into the ossification centre of the plate. In visceral view, the preorbital shows areas of cancellous spongy bone above the orbits, forming a supraorbital vault (suov, Fig. 2B), and smooth areas of bone surface for contacting the endocranium, presumed here to be mostly cartilaginous. An anteriorly facing depression (Fig. 2B, ethm.ri) is posteriorly bounded by the raised supraorbital sensory-line canal (soc) and a mesially directed ridge. Presumably, this region braced the dorsal wall of the ethmoid division of the braincase as it does in arthrodires. The lateral sides of the supraorbital sensory-line canal has a pit (Fig. 2B, pit) just posterior to the ethmoidal ridge, possibly a myodome for eyemuscle attachment. There is a broad triangular depression (Fig. 2B, dep) defined by the mesial margin of the supraorbital canal and the raised mesial edge of the supraorbital vault, and a similar posteriorly facing depression between the two converging sensory-line canals in the posterior half of the plate. The ornament of the preorbital plate is largely reticulate with patches of very fine tubercles over the orbits and towards the anterior margin.

Postorbital plate. (PtO; Figs 1A-C, 2, 3) It is only partially visible in dorsal view, showing its largest area in lateral view. Its dorsal lamina contacts the central posteriorly and is notched into the preorbital anteriorly. In lateral view, it has a smoothly concave anterior margin for the orbit and an irregularly convex posterior margin which in part forms the margin for the spiracular slit (spir; Figs 2C, 3). In visceral view, it shows no unusual features apart from linear thickenings of bone running out from the ossification centre to the margin of the spiracular slit (Fig. 3). These thickening of bone around the spiracular slit presumably assisted to direct the flow of water from outside into the spiracular groove.

Nuchal plate. (Nu; Figs 1A, B, 2A, B, D) This central median bone of the skull roof is contacted anterolaterally by the preorbitals, laterally by the centrals, and forms the posterior indented margin of the skull roof. It is a relatively small but broad bone for ptyctodontids, about half as long as the preorbital, and only a little longer than its breadth. It is quite flat. Its margins are all complete and gently concave to meet the surrounding bones which it overlaps. The confluence of the sensory-line canals on the nuchal are well-defined in dorsal view and, in ventral view, are clearly seen by the raised tubes of bone that carried the sensory-lines (pp; Fig. 2B). Weak ridges of bone radiate outwards from its ossification centre.

Left central plate. (Ce; Figs 1A-C, 2A) It is well-preserved in this specimen although only part of the right element is present, but neither shows the posteromesial margin completely preserved. It has a strongly concave anterior margin for the preorbital plate, straight contact of lateral margin where it meets the marginals, a strongly convex lateral contact margin with the paranuchal plate, and a relatively straight mesial margin where it lies in contact with the nuchal. The short region of the posteromesial margin is also quite straight and forms part of the indented posterior margin of the skull roof.

Paranuchal plate. (PNu; Figs 1A-C, 2A-D, 3) It is well preserved on the left side of the skull roof; and partly preserved on the right side. It has an irregular shape, dominated by concave margins where it contacts the postorbital anteriorly and the central anteromesially. It has short contact with the postorbital before being indented for the spiraculat slit (spir; Fig. 3). The posterior margin of the paranuchal has a large, unornamented posteriorly-facing flange of bone (art.fl; Fig. 2D) for contact with the similarly flat process on the anterior dorsolateral plate (art.con, Figs 13, 14). The ventral margin of this articulatory flange has a small foramen (for; Fig 2B), corresponding well to the position of the endolymphatic duct opening on the visceral surface of the plate in arthrodires. Yet as the plate lacks an external (dorsal opening), I conclude it is possibly just a nutritive canal. As the two articulatory surfaces of the paranuchal and the anterior dorsolateral plates do not precisely fit together, a thin pad of cartilage probably divided the two flat processes to allow some slight degree of vertical flexibility in the neck joint. There is also a smooth process of dermal bone (ppr; Fig. 2B) which projects posteriorly from the lateral margin of the paranuchal, and weakly overlaps the anterior margin of the articular process of the anterior dorsolateral plate. There is a groove along the posteroventral margin of the paranuchal plate in posterior view (Fig. 2D, gr; Fig. 6).

Marginal plate. (M; Figs 1D, E, 4, 6) It is well-preserved on the right side only. It is a wedge-shaped bone, slightly longer than the preorbitals and, with a breadth/length index of about 37, is narrower than for most other ptyctodontids. It lacks the strong inflection seen in some other forms, such as *Rhynchodus* and *Rhamphodopsis*, and is proportionately much smaller relative to the head shield than for those genera. It has an almost straight dorsal margin bordering the orbit, and relatively straight, short margins for contacting the postorbital and paranuchal plates. The visceral surface shows a pair of mesially directed laminae extending out from the centre of the plate (Fig. 4A, C, D). These laminae are triangular in dorsal view and have a roughened surface between them presumably for contact with the orbital ossification of the braincase. This structure in ptyctodontids is better preser-

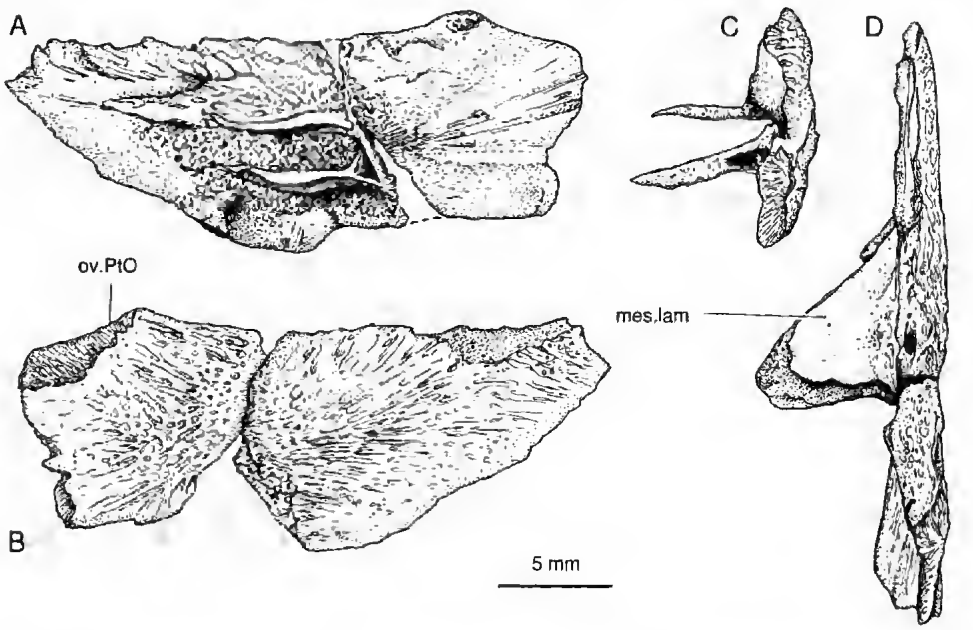

FIG. 4. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A-D**, right marginal plate; **A**, mesial view; **B**, lateral view; **C**, anterior view; **D**, dorsal view. **mes.lam**, mesial perichondral lamina extending from marginal plate; **ov.PtO**, overlap surfaces for postorbital plate.

ved in the new Gogo specimen of *Austroptyctodus* and is described in further detail below (see Figs 28, 29). The posterior division of the visceral surface of the marginal plate has a smooth triangular region emanating from behind the paired laminae. The overlap area for the postorbital plate is well-developed on the lateral surface (Fig. 4 B).

Submarginal plate. (SM; Figs 5, 6) It is preserved only for the left side, but is also well-preserved in the holotype and was figured and described by Miles & Young (1977, fig. 10). It is broad, posteriorly, narrowing to a slightly upturned, well-rounded anterior end. It is proportionately deeper in its posterior end than in all other ptyctodontids for which it is known, as in most other ptyctodontid genera it is almost bar-like. The visceral surface is smooth with the anterior end having the perichondral shell of the opercular cartilage *in situ*. In ventral view, this perichondral lamina is mesially developed into a strong process (mes.pr; Fig. 5C), which is interpreted to have supported a thick and presumably large opercular carrilage (Fig. 6).

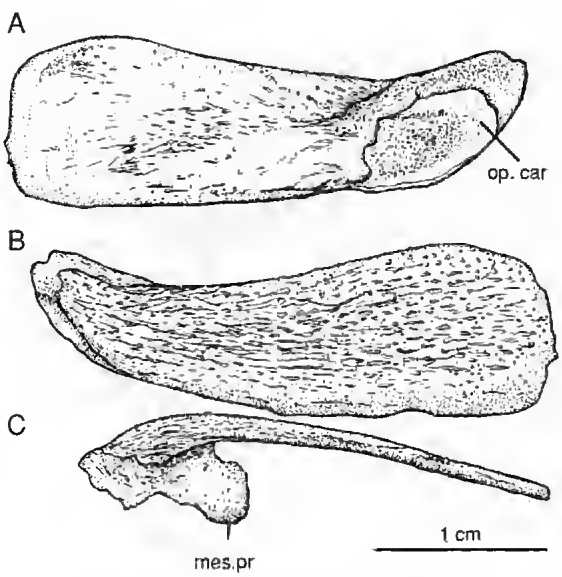

FIG. 5. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A-C**, left submarginal plate; **A**, mesial view; **B**, left lateral view; **C**, ventral view, showing opercular cartilage ossification. **mes.pr**, mesial process on opercular cartilage; **op.car**, opercular cartilage.

Visceral skeleton

Several paired and one unpaired perichondral ossification of the visceral skeleton were recovered from the specimen. Numerous visceral arch bones should be found in the skeleton of any fish that had them well-ossified, yet only a few bones have been found in this specimen, and in other articulated specimens of the Gogo form *Austroptyctodus*, and the German *Ctenurella*. This suggests that only some bones of the anterior gill arches in ptyctodontids were ossified. Schultze (1993: 213) points out that in elasmobranchs the dorsal hyoid arch elements are the first to chondrify (epihyal, ceratohyal), followed by the pharyngobranchials, epibranchials and ceratobranchials, then lastly by the hypobranchials and basibranchials. It is possible that only those elements of the first gill arch and possibly one posterior to it were invested with perichondral bone in ptyctodontids. This could be explained by the need to strengthen the bones in direct contact with the strong jaw mechanism, the more distal arch elements remaining as cartilaginous units.

The provisional identification of these gill arch elements is based on comparisons with articulared material of the other Gogo ptyctodontid, *Austroptyctodus*, as well as articulated specimens of *Ctenurella gladbachensis* in the MNHN, Paris. There is no direct evidence, because none of the smaller elements are preserved in life position in any specimen examined. The position and identification of the larger elements is based only on their general shape and articulation surfaces in relation to other large bones (*e.g.* the articular), and comparisons with the general shapes of these elements in other primitive gnathostomes (chondrichthyans, other placoderms, primitive osteichthyans).

The largest of the gill arch elements in *Campbellodus* are a pair of inwardly curved, distally broad elements. No comparable shape to bones previously identified in the ptyctodontid visceral skeleton by Watson (1934), Ørvig (1960), Gardiner (1984a) or Forey & Gardiner (1986). These bones (Fig. 7) are strongly curved mesially and have grooves for vascular or nerve passages on the lateral surface near the distal (smaller) end. They are too curved mesially and too narrow dorsally to be meckelian cartilages

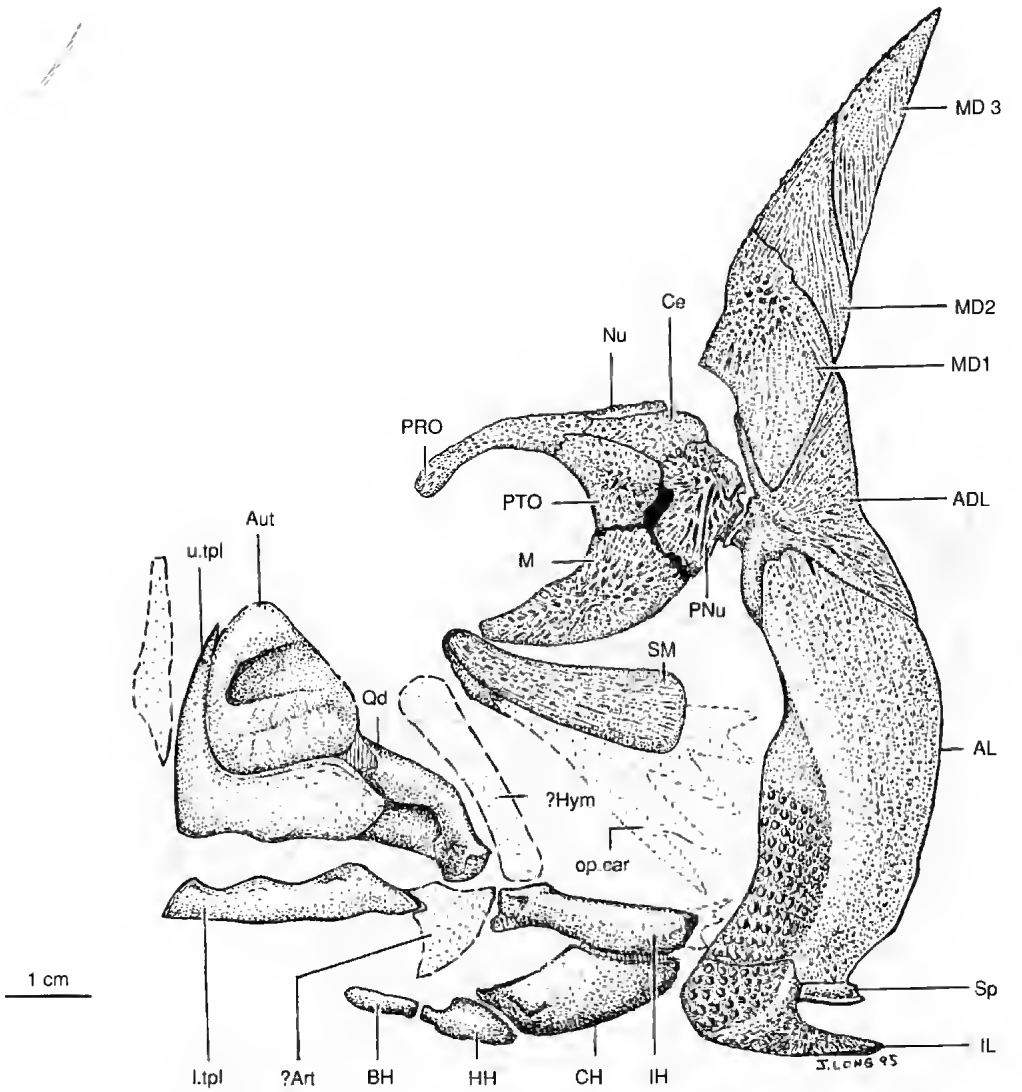

FIG. 6. — *Campbellodus decipiens* Miles *et* Young, 1977. Attempted reconstruction of dermal exoskeleton and visceral arches, from WAM 86.9.672. Stippled areas are hypothetically restored cartilage bones. **ADL**, anterior dorsolateral plate; **AL**, anterior lateral plate; **Art**, articular; **Aut**, Autopalatine; **BH**, basihyal; **Ce**, central plate; **CH**, ceratohyal; **HH**, hypohyal; **Hym**, hyomandibular; **IH**, interhyal element; **IL**, interolateral plate; **l.tpl**, lower tooth plate; **M**, marginal plate; **MD**, MD1, 2, 3, median dorsal plate(s) or spines; **Nu**, nuchal plate (posterior element); **op.car**, opercular cartilage; **PNu**, paranuchal plate; **PRO**, preorbital plate; **PtO**, postorbital plate; **Qd**, quadrate; **SM**, submarginal plate; **Sp**, spinal plate; **u.tpl**, upper tooth plate.

supporting the toothplates. By comparison with other gnathostome fishes they could be ceratohyals, which are also large, flat bones with mesial curvature in primitive osteichthyans like *Medoevia* (Lebedev 1995), *Glyptolepis* (Jarvik 1972) or primitive lungfishes (Miles 1977; Campbell & Barwick 1988). However it is noted that the presence of an expanded ceratohyal is regarded as a synapomorphy of higher osteichthyans (Gardiner 1984b) as the condition in acanthodians (Miles 1973) or primitive actinopterygians (Gogo palaeoniscoids, Gardiner 1984b) is to have a slender rod-like ceratohyal of similar form to the ceratobranchials.

What therefore is the evidence for calling the elongate bone, bracing the articular in *Ctenurella*

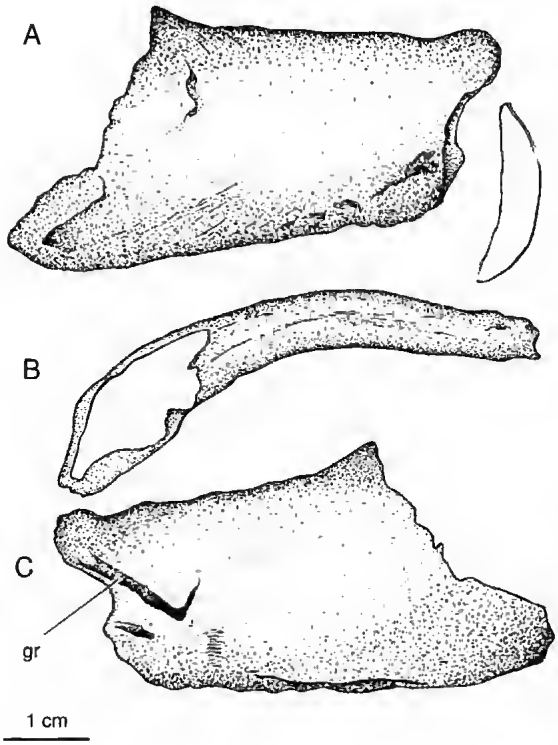

FIG. 7. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A-C**, left ceratohyal; **A**, mesial view; **B**, dorsal view; **C**, left lateral view. **gr**, groove.

gladbachensis, a "ceratohyal" (*e.g.* Forey & Gardiner 1986)? The bone lies ventral to the inferred position of the dorsal hyoidean bone, which would primitively lie next to the quadrate, and is a large bone with a complex proximal head. As restored by Forey & Gardiner (1986), it would distally meet with the restored hyomandibular and form part of a normal hyoidean arch system, except for the fact that it braces the jaw joint rather than carries on ventrally to the basihyal or hypohyal bones. In this respect it would be unique amongst vertebrates if regarded as a ceratohyal. I propose an alternative explanation: the elongated bone with an expanded double articulatory head, which braces the lower jaw, is a specialised interhyal (or "symplectic" in the terminology of Veran 1988, but not homologous with the symplectic of higher actinopterygians). Thus I regard the broad, expanded bones in *Campbellodus* as true ceratohyals that have independently acquired the derived condition of being expanded for larger attachment area of the depressor mandibulae and interhyoideus muscle groups. Such an adaptation would benefit a specialised feeding mechanism as it occurs in ptyctodontids which were strong biters (in the ecomorphological context of Liem 1993) and thus required extreme modifications of the jaw musculature system to increase biting pressure, relative to the conservative muscle systems hypothetically restored in other placoderms such as arthrodires (*e.g.* Stensiö 1963; Long 1995a).

The visceral skeleton is virtually unknown in all other placoderms, apart from a serial grinding series by Stensiö (1963, fig. 8) showing only the ventral gill arch system in the arthrodire *Tapinosteus*. Thus the presence or absence of an interhyal in other placoderm groups is unknown. The function of this unusual arrangement for the expanded interhyal in ptyctodontids can only be suggested as an attachment brace for supporting the large opercular covering over the branchial lamina, possibly by attachment of additional cartilaginous opercular elements (as in the opercular cartilages of chimaetids which emanated from both the epihyal and ceratohyal elements; e.g. *Rhinochimaera* and *Callorhynchus*, Jarvik 1980, vol. 1, figs 299, 303).

The next largest bones in the visceral skeleton of *Campbellodus* are elongated paired bones with an expanded head (Fig. 8), directly comparable with the elements identified as ceratohyals by Forey & Gardiner (1986), and found in the new Gogo specimen described below, and also in articulated position in *Ctenurella gladbachensis* (see below, Fig. 25). These are not interpreted as epihyals (= hyomandibular) because of the presence of a separate epihyal in position on the new specimen of *Austroptyctodus* (Fig. 29, Hym). I regard these as interhyal elements which braced the lower jaw joint (Fig. 6, IH), the ventral most articular head meeting the small articulation surface described on the articular bone in *Austroptyctodus* (Miles & Young 1977, "arthy", fig. 24). There is a well defined foramen at this articular head (for; Fig. 8) which may have transmitted the hyomandibularis nerve. The narrow distal end of the bone is compressed laterally and ends in a slit-like articulation surface (shown in Fig. 8E), presumably for

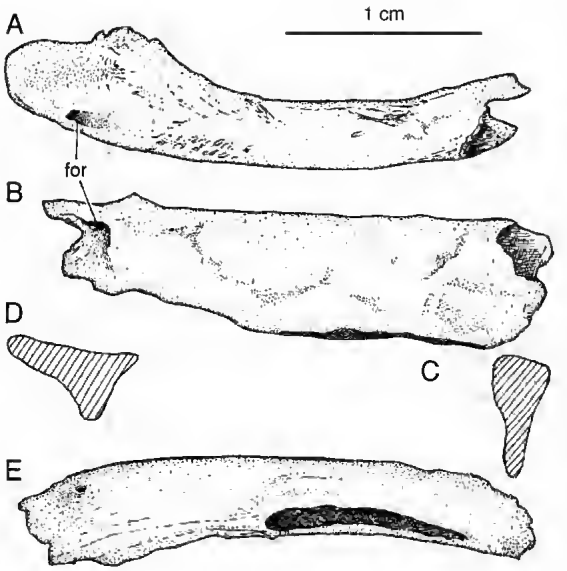

FIG. 8. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A-D**, left interhyal; **A**, dorsal view; **B**, left lateral view; **C**, **D**, cross-sections of the interhyal, respectively in distal and proximal sections; **E**, ventral view. **for**, foramen.

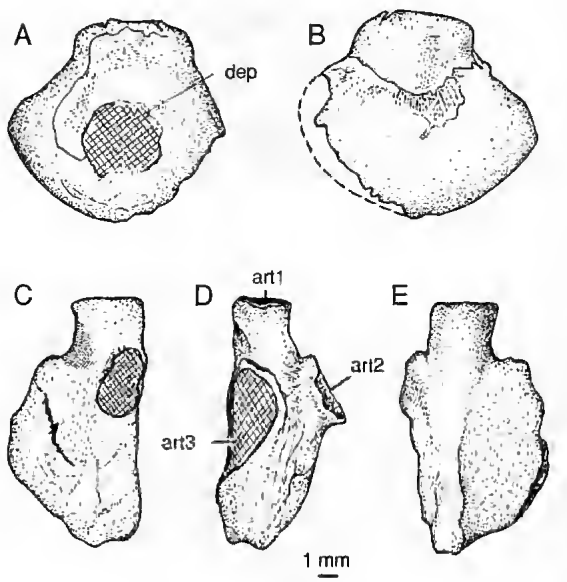

FIG. 9. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A**, **B**, basihyal; **A**, ventral view; **B**, dorsal view. **C-E**, hypohyal; **C**, mesial view; **D**, dorsal view; **E**, lateral view. **art**, articulation facets; **dep**, depression.

contacting the similar-sized articulation area on the ceratohyal. Two small paired elements having three articulation surfaces are here identified as possible hypohyals (Fig. 9C-E). They are flask-shaped elements with a small anterior (?) articulation surface (art 1), and two much presumed larger, mesial (art 2) and dorsal (art 3) articulation facets. The presumed dorsally-facing articulation surface is the largest of the three and matches closely with the long ventral articulation facet on the distal end of the ceratohyal. The second largest articulation is here assumed to be for mesial contact with the opposing hypohyal, as in many modern selachians (e.g. *Chlamydo-selachus*, Smith 1937). They compare well to the basic pattern of hypohyals seen in early osteichthyans (Gardiner 1984b; Lebedev 1995).

A small unpaired bone, presumably the median hyoid arch element or basihyal (Fig. 9A, B), is an almost circular bone with a single protruding articulation facet, giving it the overall shape of a circular water-canteen. This bone was identified by Gardiner (1984a, fig. 3) and by Forey & Gardiner (1986) in *Austroptyctodus* as the urohyal, yet this identification was based only on its overall shape as it was found only in one specimen, and in which case the gill arch bones were not in natural articulation. The author's identification of the element as a basibranchial is based on the fact that only one large median element of the ossified hyoid arch is present in *Campbellodus*, and that bone is therefore most likely to be the basihyal. Its rounded overall morphology is similar to that of the osteolepiform *Medoevia* (Lebedev 1995). The single articulatory facet faced posteriorly and accommodated the smaller anteriorly facing articulatory surfaces on the hypobranchials, or alternatively, may have met with a second smaller medial basibranchial element.

Dentition and jaw cartilages

The toothplates and jaw cartilages of *Campbellodus* have been well-described and figured by Miles & Young (1977), and Long (1988b) described an isolated upper jaw toothplate of *Campbellodus* sp. from the slightly younger Napier Range, to the west of Fitzroy Crossing. New material of *Campbellodus* showing the

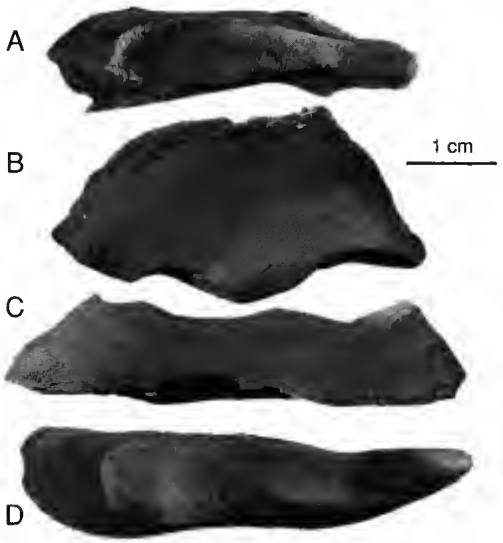

FIG. 10. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 95.6.112. **A**, **B**, upper toothplate, **A**, ventral view; **B**, mesial view; **C**, **D**, lower toothplate; **C**, mesial view; **D**, dorsal view. Whitened with ammonium chloride.

upper and lower toothplates (WAM 95.6.112) is shown here (Fig. 10), but adds no further information to the published description. The tooth plates had a crushing action with the posterior end of each tooth plate being broadest and thickest, and increased wear on the tooth plates result in differing morphologies, especially for the upper tooth plate, as noted by Miles & Young (1977: 150). A most peculiar feature of the dentition is that the lower toothplate extends anteriorly well forward of the anterior margin of the upper tooth plate when they occlude, as shown in the reconstruction (Fig. 6).

Left quadrate. (Figs 1K, 11) It is well-preserved in WAM 86.9.672. It is a robust perichondral ossified shell consisting of a main division with an inner flange, as described for *Austroptyctodus gardineri* (Miles & Young 1977, figs 24, 25). The main shaft is flat in cross-section with a broad articular end. Lateral to the articular surface (art.md) is a break in the perichondral bone surrounded by a thickening around it. This process (pr.det) is possibly a homologue with the "detent process" on the posterolateral region of the quadrate in arthrodires (e.g. *Goujetosteus pulchellus*, Gardiner & Miles 1990, fig. 20; *Menamaraspis*, Long 1995b, fig.16). This raises the question of whether the "detent process" on the quadrate of ptyctodontids is actually homologous to that of arthrodires or corresponds to one of the several palatobasal articulations with the endocranium seen on the quadrate or palatoquadrate of other primitive placoderms (e.g. *Romundina*, Young 1986, fig. 12C). The function of the detent process in arthrodires is to limit movement or lateral slip of the jaw joint. This is clearly seen by physically moving the lower jaws and fixed cheek units against one another in well-preserved Gogo arthrodires. In acanthothoracids and rhenanids, the palatobasal and nearby articulatory facets on the palatoquadrate were for attachment to the endocranium. In *Campbellodus* the quadrate is situated a considerable distance ventral to the extent of the braincase as deduced from similar positions of the endocranial ossifications and jaws in *Austroptyctodus* n.g., and thus the process in ptyctodontids is here seen to be homologous to the detent process in arthrodires, a constraint to lateral movement during opening and closing of the jaws. The large well-defined cavity for the posterior division of the adductor mandibulae muscles (add.foss) is seen in mesial view (Fig. 11B). The ventral surface of the quadrate (Fig. 11C) is relatively flat to weakly concave. It shows a roughened muscle or ligament attachment area (m.att) immediately anterior to the articulation area which may have been for the mandibulohyoid ligament.

The articular is not preserved in any of the *Campbellodus* specimens, but the autopalatine ossification is known from the holotype, and has been described and figured by Miles & Young (1977, fig. 11, pl. 2B).

Trunk shield

The trunk shield of *Campbellodus* (Figs 6, 12, 14) comprises large paired anterior lateral plates, paired anterior dorsolaterals, three median dorsal elements, the most distal of which is developed as a median spine, a pair of large interolateral plates, paired small spinal plates, and a small anterior median ventral plate. The restored trunk shield (Figs 6, 14) is similar to that of *Rhynchodus tetrodon* in having a very extensive branchial lamina on the anterior laterals and interolaterals with large hooked stellate tubercles,

but differs from all other known ptyctodontids in having three median dorsal bones, and distinctly small spinal plates.

Median dorsal plates. (MD1; Fig. 1H) Situated ventrally it straddles the anterior dorsolaterals and is a thin bone lacking a median ventral keel, as in *Rhamphodopsis*, *Chelyophorus*, *Ctenurella* and *Austroptyctodus* (*e.g.* Miles & Young 1977, fig. 29 D). It is the largest of the three dorsal trunk bones and has a strongly convex anterior margin that slightly overhung the nuchal gap of the head shield when the head was fitted onto the articulated trunk armour. It has a small dorsal overlap flange for the second median dorsal plate (MD2; Fig. 1G). This plate is slightly more elongated that the main median dorsal, and also has a short, narrow overlap shelf on its postero-dorsal margin for the median dorsal spine. This spine (MD3; Fig. 1F) is similar to that figured by Miles & Young (1977, fig. 13) for specimen NHM P50907. It is a hollow bone with a grooved posterior face and has only few scattered tubercles on its surface, unlike the strongly developed dermal ornamentation in the spines of *Rhamphodopsis* and *Ptyctodopsis*.

Anterior dorsolateral plate. (ADL; Figs 12-14) It is of regular shape for ptyctodontids, not unlike that of *Ctenurella* or *Rhynchodus*. It has a well-

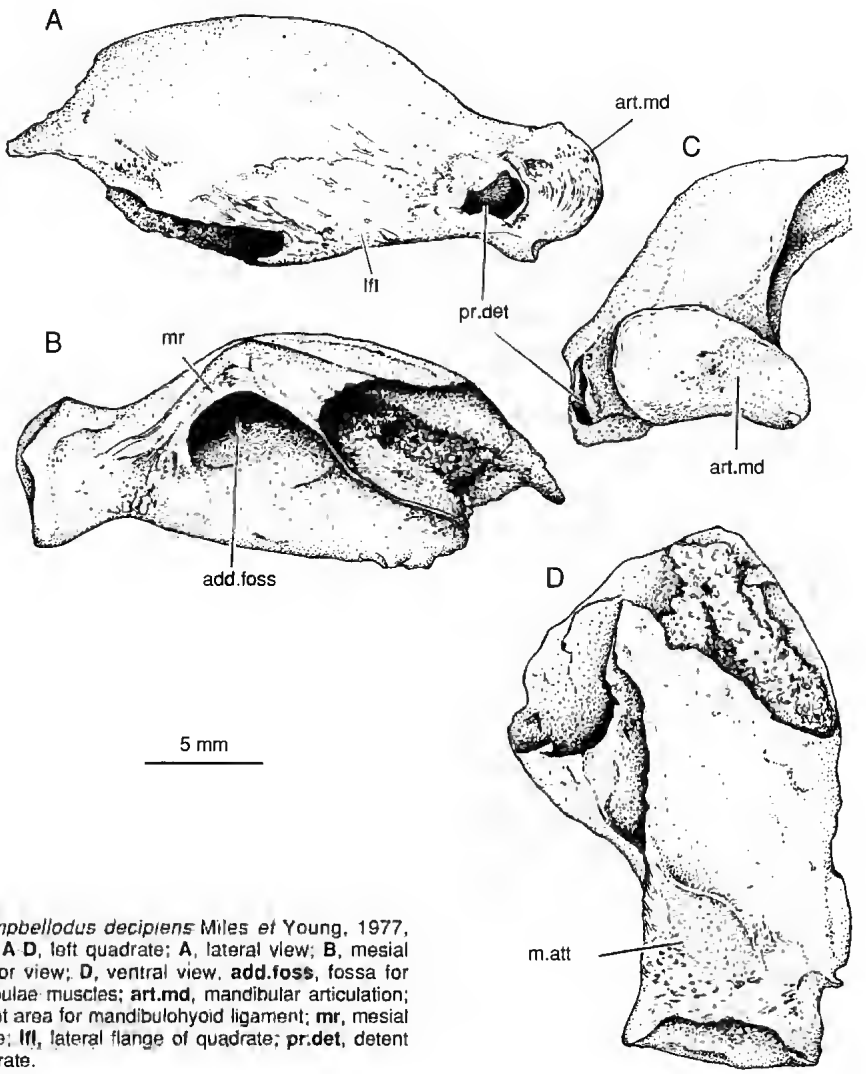

FIG. 11. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A-D**, left quadrate; **A**, lateral view; **B**, mesial view; **C**, posterior view; **D**, ventral view. **add.foss**, fossa for adductor mandibulae muscles; **art.md**, mandibular articulation; **m.att**, attachment area for mandibulohyoid ligament; **mr**, mesial ridge of quadrate; **lfl**, lateral flange of quadrate; **pr.det**, detent process on quadrate.

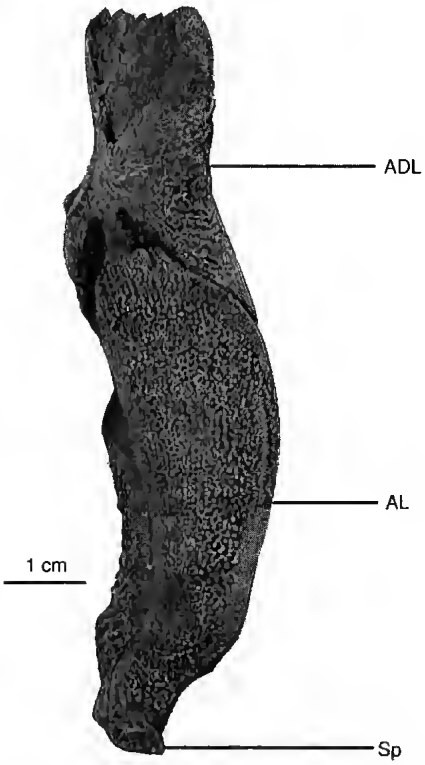

Fig. 12. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. Partially articulated trunk shield in left lateral view. **ADL**, anterior dorsolateral plate; **AL**, anterior lateral plate; **Sp**, spinal plate.

developed anterior ventral process of ornamented dermal bone that meets the anterior lateral plate (v.pr; Fig. 13), and the main lateral-line sensory canal (llc) passes through a tube within the bone and is not externally visible, nor is it expressed as a thickened tube on the visceral surface of the plate as occurs in ptyctodontid head shield bones. The articular condyle (art.con) for the neck joint is a broad flat surface with a weak median ridge which is hardly visible in lateral view (Figs 13, 14). Noticeable difference in the anterior dorsolateral plate of *Campbellodus* to those of other ptyctodontids is that it lacks the distinct angular inflection seen in the anterior dorsolateral plate of *Rhynchodus tetrodon* (Gross 1933, pl. 10, figs 2-4) or *Chelyophorus verneuili* (pers. obs.). It is broadest about two-thirds down its height from its dorsal margin, unlike the dorsally broader plate in *Austroptyctodus* (Miles & Young 1977, fig. 30), and the externally exposed region is noticeably broader in its ventral division than in either *Ctenurella* or *Rhamphodopsis*. The overlap area for the median dorsal 1 plate (ov.MD) is much smaller than the large ventral overlap surface for the anterior lateral plate (ov.AL).

Anterior laterals. (AL; Figs 6, 12, 14) These are the largest bones of the dermal skeleton, as in all ptyctodontids. The dorsal region of the plate is very broad, being approximately three times the width of the narrow ventral division of the lateral lamina. The dorsal region of the anterior margin of the bone is strongly concave where the postbranchial lamina (Fig. 14, b. lam) begins. It has a well-defined lateral lamina with finely ornamented rugose dermal bone, merging mesially into the extensive flat postbranchial lamina covered with well-ordered rows of large, triangular pectinated tubercles. Each of these tubercles has a spray of about five or six inwardly pointed tips, the central one being the largest, and the head of the tubercles facing towards the centre of ossifi-

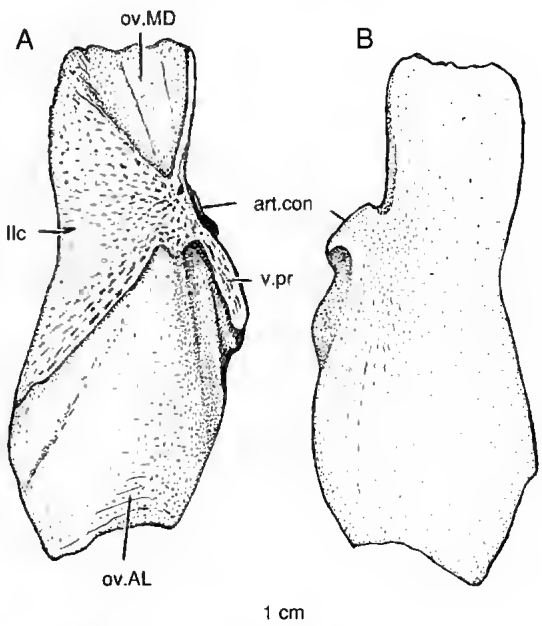

Fig. 13. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A**, **B**, anterior dorsolateral plate; **A**, right lateral view; **B**, mesial view. **art.con**, articular condyle or face on ADL plate; **llc**, main lateral line canal; **ov.AL**, overlap surfaces of anterior lateral plate; **ov.MD**, overlap surfaces of median dorsal plate; **v.pr**, ventral process of ornamented bone on anterior dorsolateral plate.

cation of the bone, close to its spinal margin. Miles & Young (1977, figs 1, 2F, pl. 4A) showed part of this postbranchial lamina on the type specimen, and figured a scanning electron micrograph showing clearly the morphology of one of these tubercles. The contact margin for the spinal plate is a short, straight horizontally-directed edge of bone above the embayed margin for the pectoral fin.

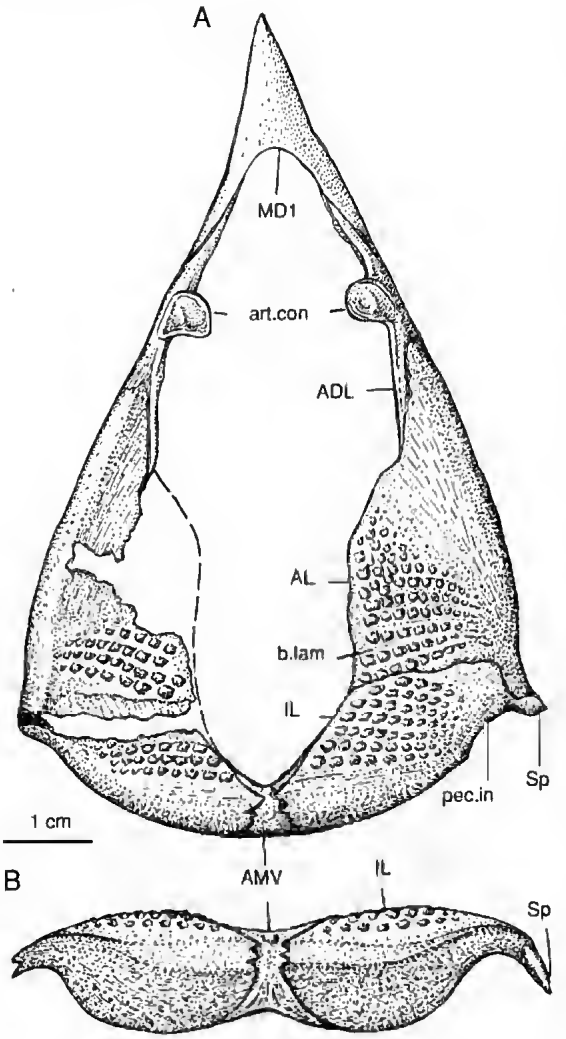

FIG. 14. — *Campbellodus decipiens* Miles et Young, 1977, WAM 86.9.672. **A**, **B**, trunk shield; **A**, anterior view; **B**, ventral view. **ADL**, anterior dorsolateral plate; **AL**, anterior lateral plate; **AMV**, anterior median ventral plate; **art.con**, articular condyle or face on ADL plate; **b.lam**, branchial lamina of trunk shield; **IL**, interolateral plate; **MD1**, median dorsal plate; **pec.in**, pectoral fin incision on trunk shield; **Sp**, spinal plate.

Unlike the condition in most other placoderms where the spinal plate projects anteriorly to the pectoral fin, it is clear that in *Campbellodus* the spinal plate is immediately dorsal to the main embayment in the trunk shield lateral lamina. The position of the scapulocoracoid in *Austroptyctodus*, also showing the fin emerged below the junction of the anterior lateral and the interolateral, confirms that the pectoral fin did emerge ventral to the position of the spinal in *Campbellodus*.

Spinal plate. (Sp; Figs 6, 12, 14) This small bone, with a very short projection of the posteriorly-facing spinal process, contacts the anterior lateral along almost all of its dorsal margin, but has only a very short anterior connection with the interolateral plate. In internal view, the spinal plate is hollow. It has been previously identified and described for the NHM P50907 by Miles & Young (1977, fig. 12).

Interolateral plates. (IL; Figs 6, 14) These consist mostly of the anteriorly facing postbranchial lamina, with no external lateral lamina. The ventral laminae (Fig. 14B) are well-developed as in all ptyctodontids and meet the anterior median ventral bone mesially, not contacting each other as occurs in *Rhynchodus tetrodon* (Gross 1933). As noted for the spinal, they have a well-defined pectoral incision for the pectoral fin (pec.in; Fig. 14A), and ventrally broaden out mesially. The postbranchial lamina has a strongly convex contact margin with the anterior lateral plates, similar to the condition in both *Rhynchodus* and *Austroptyctodus*.

Anterior median ventral plate. (AMV; Fig. 14 A, B) Unusually broad, it is more than twice as broad as its length, although its externally exposed surface in the articulated armour is very narrow. Most of its breadth is for the overlap laminae for the interolateral plates, and these surfaces have a fluted bone texture. The anterior margin of the plate is quite straight, unlike the V-shaped anterior median ventral plate in *Chelyophorus*.

Pelvic girdle and endoskeleton

The pelvic girdles are well-preserved in the specimen showing two principal components, the dermal pelvic bones and associated endogirdle,

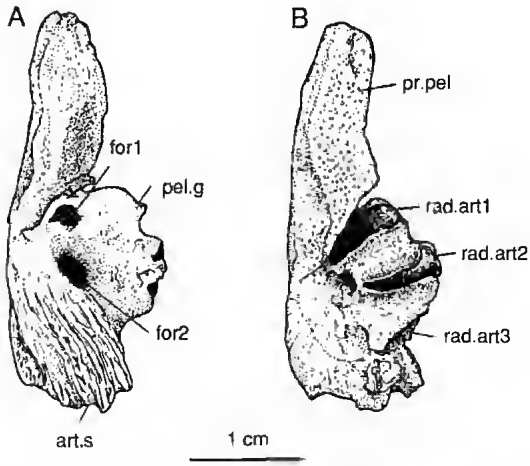

Fig. 15. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A**, **B**, prepelvic bone and associated endoskeletal pelvic girdle; **A**, dorsal view; **B**, ventral view. **art.s**, articulation scars for mesial attachment; **for**, for 1, 2, foramen or identified series of foramina; **pel.g**, groove between basal articulations on pelvic endoskeletal ossification; **pr.pel**, dermal process of pelvic girdle; **rad.art**, 1, 2, 3, articular facets for fin radials.

and a pair of asymmetric large, smooth basal plates for the pelvic fin, similar to the element described in the female specimens of *Rhamphodopsis threiplandi* (Miles 1967, figs 13, 15).

External pelvic girdle. (Figs 1I, J, 15, 17) It has a large, narrow ventrolateral lamina with external ornament matching that of the dermal bones and scales. This part (pr.pel; Fig. 15) is probably equivalent to the paired prepelvic bones lying anterior to the pelvic fins in *Rhamphodopsis*, although the associated endoskeletal girdle is not known in that form. In the new specimen the perichondrally ossified endogirdle shows three large, elongated articulation surfaces for the pelvic fin radials (rad.art 1-3; Fig. 15), with two large foramina (for1, 2) between the fin attachment surface and the outer dermal bone, for the passage of nerves, veins and arteries to the pelvic fin. Musculature of the pelvic fin probably attached to the roughened area surrounding these foramina and to the dermal component of the pelvic girdle. These paired elements met mesially by a roughened connection area (art.s) with an interdigitating suture (Fig. 17). The smooth surface surrounding this connective region was no doubt covered with muscle or ligamentous connection in life. When the two parts of the pelvic girdle and endogirdle are reassembled in this way, the dermal prepelvic bones are not seen to have any mesial contact, as seen in *Rhamphodopsis*, but are widely separated. In restoring the pelvic girdle and endogirdles (Fig. 17), the bones were assembled with plasticine holding the basal plates together and then matched up with the posterior width of the trunk shield, so that the estimated width of the prepelvic bones correlated with the natural curvature of the body.

Fin basal plate. The large fin basal plate (Fig. 16) is represented by both left and right elements, although, as prepared, it is not known which is which. The element has strong curvature in both mesial-lateral direction and rostrocaudad, unlike in *Rhamphodopsis* specimens, in which it seems to be a flat, subtriangular bone. Along its inner ventral margin is a well-developed ridge (ri; Fig. 16A), presumably for insertion of the large pelvic scales along a broad, smooth flange (fl). A roughened area (r.a) is seen next to the centrally raised median area, presumably for attachment of ligaments and scales of the lateral flank of the fish. The visceral surface is smooth but has a

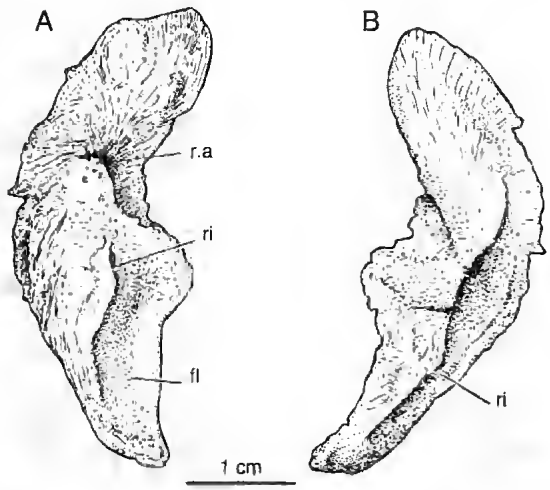

Fig. 16. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A**, **B**, right female pelvic basal plate; **A**, ventral view; **B**, dorsal view (slightly oblique, see figure 17 for possible orientation with respect to prepelvic bones and pelvic girdle). **fl**, flange; **r.a**, articulatory ridge on pelvic basal plate; **ri**, ridge for scale overlap on pelvic basal plate.

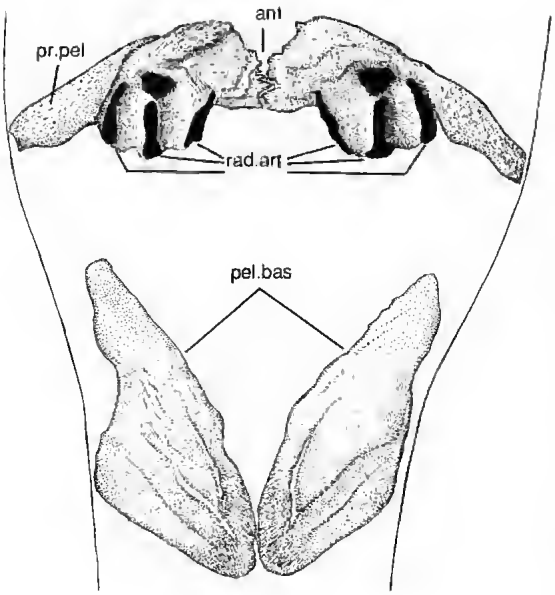

FIG. 17. — *Campbellodus decipiens* Miles *et* Young, 1977. Reconstruction of pelvic region of a female showing possible orientation of prepelvic bones, pelvic girdle and pelvic basal plates, ventral view; **ant**, anterior direction; **pel.bas**, pelvic basal bone (female basal ossification); **pr.pel**, dermal process of pelvic girdle; **rad.art**, 1, 2 articular facets for fin radials.

well-defined ridge (ri; Fig. 16B) running along its ventral lamina.

Scapulocoracoid?

A poorly preserved part of a perichondral ossification showing what appears to be a glenoid facet is here shown in figure 18 (glen), although, as most of the bone is missing, its identification is uncertain. It is possibly part of the scapulocoracoid from the shoulder girdle, or alternatively may be a piece of the occipital ossification of the endocranium, as described below in *Austroptyctodus*.

Axial skeleton

The vertebral column comprises the synarcual (Fig. 19) and numerous paired perichondral elements that straddled the cartilaginous notochord, as described for *Rhamphodopsis* (Miles 1976), *Ctenurella gladbachensis* (Ørvig 1960), and similar to the vertebral ossifications seen in other placoderms (e.g. *Coccosteus*, Miles & Westoll 1968; *Austrophyllolepis*, Long 1984b; *Incisoscutum*, Dennis-Bryan & Miles 1981; *Eastmanosteus*, Dennis-Bryan 1987). Some of the haemal arch elements have reasonably long ventral processes compared to those seen in *Ctenurella* or *Rhamphodopsis*.

Synarcual. It is similar to that described for *Austroptyctodus* (Miles & Young 1977, fig. 32), showing clearly the notochordal groove (not.gr; Fig. 19) canal for the spinal cord (sp.c) and lateral

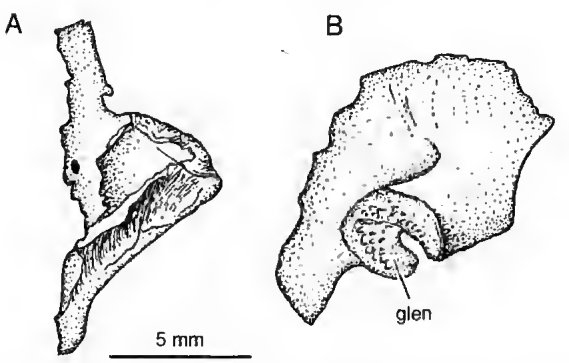

FIG. 18. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. Possible right scapulocoracoid ossification (incomplete). **glen**, glenoid condyle of endocranium.

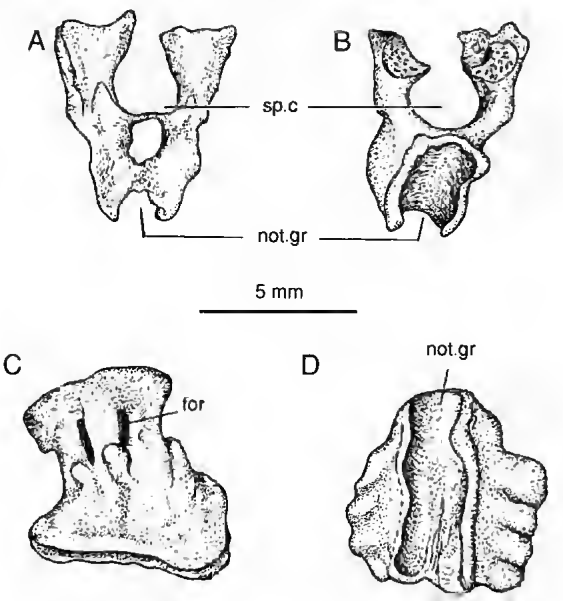

FIG. 19. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A-D**, synarcual; **A**, anterior view; **B**, oblique posterior view; **C**, lateral view, **D**, ventral view. **for**, foramen or identified series of foramina; **not.gr**, notochordal groove; **sp.c**, spinal cord canal.

FIG. 20. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. **A**, dermal scale showing overall shape; **B**, detail of externally ornamented area of same scale. SEM photomicrographs.

slit-like foramina (for) for the spinal nerve roots. Large basal elements for the median fins are found in the material and in general outline match those described for *Austroptyctodus* (Miles & Young 1977, figs 33, 34). In addition there is a posteriorly situated second median dorsal bone that bears a close resemblance to the median dorsal 1 of the trunk shield. As for *Ctenurella gladbachensis*, this is presumed to be the dorsal spine preceding the second dorsal fin.

Squamation

The specimen contained many hundreds of scales distributed throughout the nodule, and not concentrated specifically around the pelvic girdle. Thus, as in the articulated specimen of *Austroptyctodus* described below, in which ordered scale rows are seen on the flank of the trunk region, the whole of the body posterior to the trunk shield is assumed to have been covered by large overlapping scales. Each scale has an ornamented external region which is subrectangular in form but quite variable as to precise shape (Figs 20, 21) and a large, ventrally-facing smooth overlap surface. The scales are macromeric, from their large size and the relative size of the neural arch elements it is suggested that there was a correspondence of one scale row per somite, and that they were ordered in neat rows with large overlapping ventral flanges.

Long (1995b: 110) gives an attempted life restoration of *Campbellodus decipiens* based on the new material described herein.

REVISION OF THE GENUS *Ctenurella* Ørvig, 1960

Although the original description of *Ctenurella gladbachensis* by Ørvig (1960) did not recognise the presence of the submarginal bone, this was soon corrected along with further observations of the material by him (1962). Another peculiarity of *C. gladbachensis* noted from Ørvig's description is the purported absence of the anterior median ventral plate, present in all other ptyctodontids where the armour is well-preserved, including *C. gardineri* (Miles & Young 1977, fig. 31). His last reconstruction of the head of *C. gladbachensis* was modified to show broader anterior margins on the preorbital plates and was subsequently adopted by Stensiö (1969, fig. 40A) and used by Ørvig (1971) and Miles & Young (1977, fig. 15). It incorporated a smaller dermal bone anterior to the marginal plate (a possible suborbital bone).

Denison (1978, fig. 3B) attempted to reconstruct parts of the visceral skeleton of *C. gladbachensis*, adding the hyomandibular as an anteroventrally directed bone, bracing the jaw articulation and meeting with an opercular cartilage. Forey & Gardiner (1986) described a new specimen of the Gogo "*Ctenurella*" and figured newly prepared NMH specimens of *C. gladbachensis* in which the "ceratohyal" was clearly identified.

Original specimens in the MNHN, Paris, include articulated individuals showing details of the skull roof, jaws and visceral skeleton (Fig. 22) and one superb specimen, both part and counterpart (Figs 23, 24B, 25), meticulously prepared by Dr. D. Goujet, showing the dermal bones of the skull and trunk shield, as well as jaws and associated ossifications, the hyoid elements, ros-

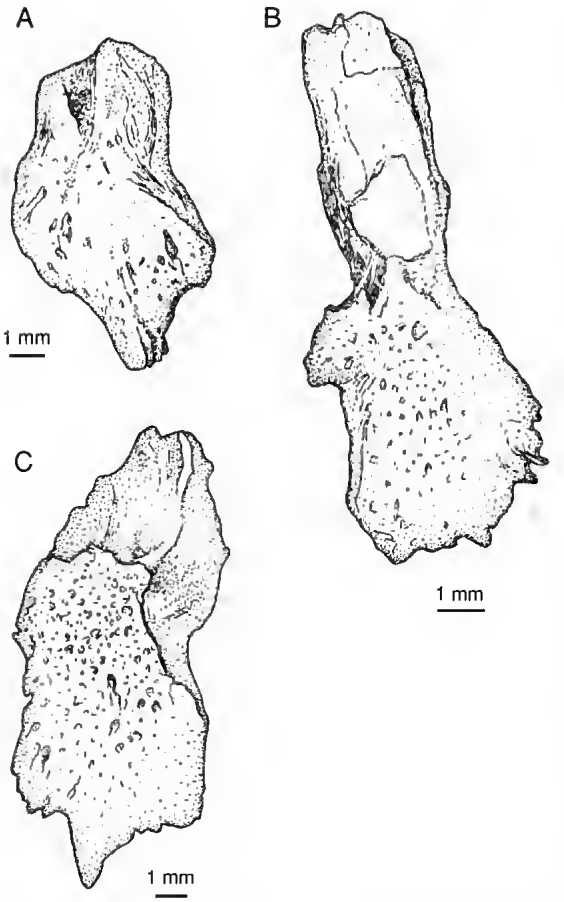

FIG. 21. — *Campbellodus decipiens* Miles *et* Young, 1977, WAM 86.9.672. Dermal scales. **A**, basal view; **B**, **C**, coronal views.

tral cartilages and other visceral arch elements. Four well-preserved specimens were studied in order to determine the nature of the hyoid arch bones, the jaw cartilages and the reconstruction of the head shield. The new specimens examined at the MNHN, Paris, corroborate the orientation of the interhyal bone, as observed by Forey & Gardiner (1986, called the "ceratohyal") in its posteroventrally slanted position behind the articular, as seen also in *Austroptyctodus* (Figs 28, 29). Closer examination reveals that the expanded head of the interhyal in *C. gladbachensis* only makes contact with the posterior margin of the articular and does not meet with the posterior edge of the quadrate (Fig. 25).

The skull roof is well-preserved in the NHM specimens but differs in several respects from the reconstructions given by Ørvig (1960, 1971), Stensiö (1969), Miles & Young (1977) and Denison (1978). In all four of the NHM specimens examined, the central plates meet each other behind the nuchal plate, unlike the condition in both the Gogo ptyctodontids, in which the nuchal forms the median posterior margin of the head shield (Figs 23, 25B). The anterior margin of the head shield is relatively broad and straight with the pineal bone tightly enclosed by the anteromesial corners of the preorbital plates. The closure of the central plates to form the posterior margin of the head shield in *Ctenurella gladbachensis* is also hinted at in the one skull figured by Ørvig (1960, pl. 26, 1, 2) where the left central plate protrudes behind the nuchal plate. The pineal plate is always firmly enclosed by the preorbital plates with only a short anterior margin forming the anterior border of the head shield, unlike the Gogo form which has a pineal plate significantly smaller than the gap defined for it by the preorbitals.

Thus, a new reconstruction of the skull roof of *Ctenurella gladbachensis* is presented here (Fig. 26B) which shows noticeable differences to the Gogo specimens.

It is noted that the sclerotic ring, not previously described for ptyctodontids, is well preserved in one Bergisch-Gladbach specimen, and shown clearly in figure 22A (bottom right corner above the lower tooth plate). It comprises four sclerotic bones and matches closely with the supraorbital vault defined by the preorbital and postorbital plates.

The lower tooth plates of *Ctenurella gladbachensis* have a well-developed ventral process (Figs 22A, 25), a feature also seen in the Gogo *Austroptyctodus* (Fig. 34; Miles & Young 1977, pl. 5B). Futther differences between *Ctenurella* and *Austroptyctodus* are seen in the median dorsal plates. In *Ctenurella* (Fig. 22A) it has weakly convex lateral margins and the posterior margin even has a taper to a posterior point. In *Austroptyctodus*, the median dorsal plate has a much broader anterior margin than its posterior margin, weakly concave lateral margins and a more strongly developed posterior process (Miles & Young 1977, fig. 29D).

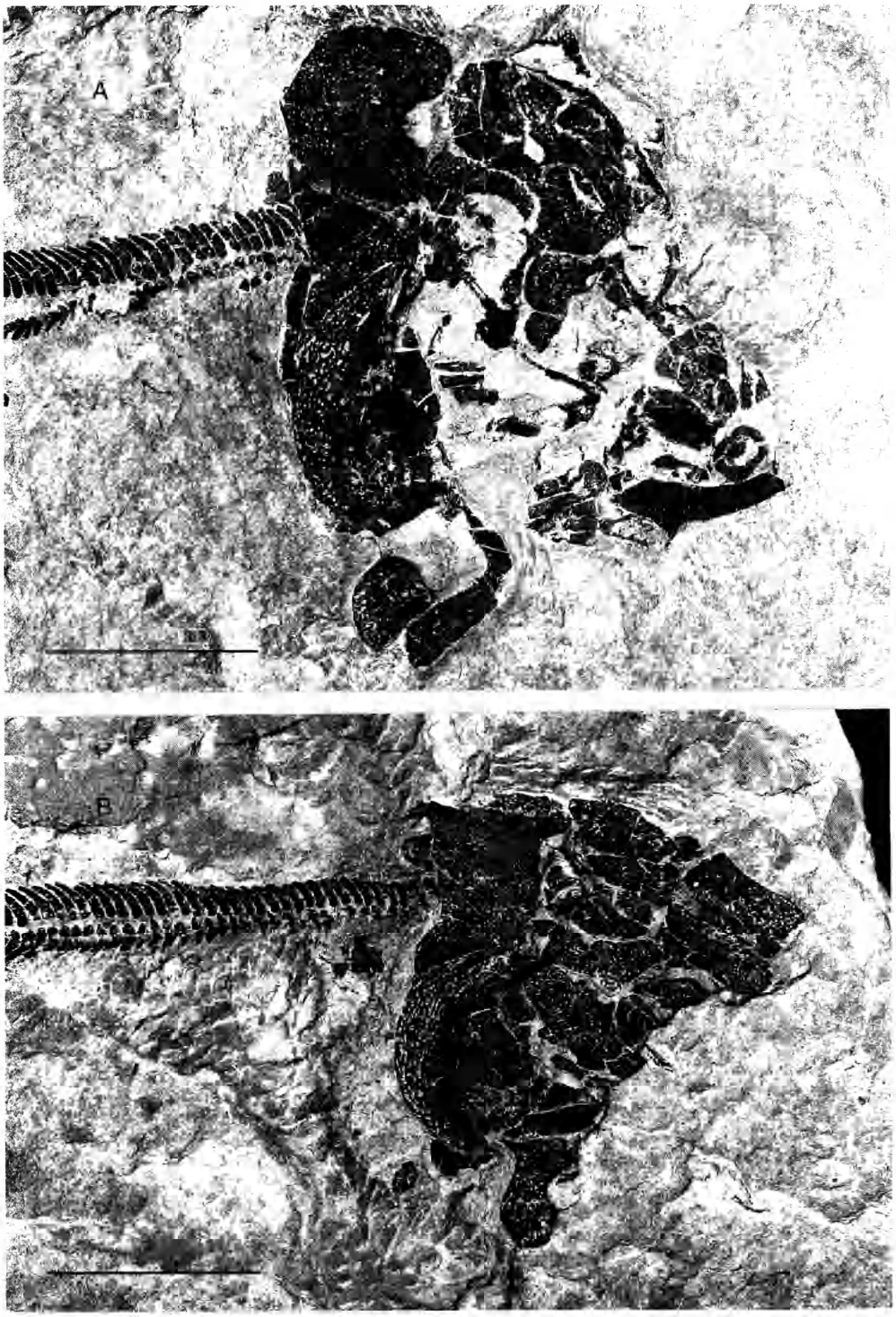

FIG. 22. — *Ctenurella gladbachensis* Ørvig, 1960. Specimens in the palaeontological collections of the Muséum national d'Histoire naturelle, Paris. **A**, MNHN ARD 229, note presence of small sclerotic ring near lower jaw tooth plate, **B**, MNHN ARD 231. Scale bar: 1 cm.

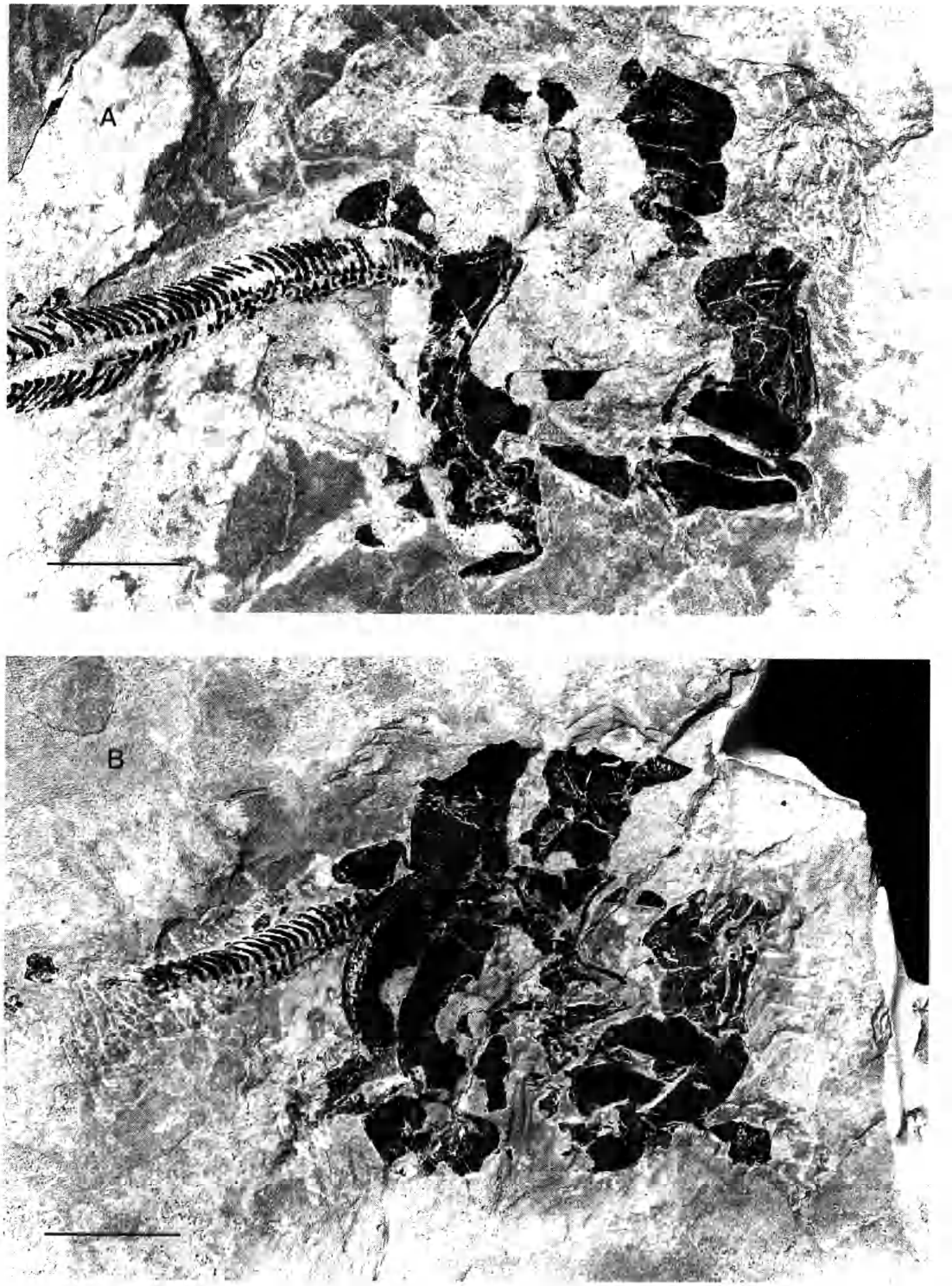

FIG. 23. — *Ctenurella gladbachensis* Ørvig, 1960. Specimens in the palaeontological collections of the Muséum national d'Histoire naturelle, Paris. **A**, MNHN ARD 230; **B**, MNHN ARD 233. Scale bar: 1 cm.

Amended generic diagnosis

A small ptyctodontid with a nuchal completely enclosed by the centrals and preorbitals; preorbitals meet in midline and suture with the pineal; nuchal plate anteriorly pointed. Marginal plates with well-developed ventral process. Toothplates of the shearing type, lower tooth plates having a well-developed ventral process near the articular end. Trunk shield lacking a spinal plate, median dorsal plate approximately as broad as long, lacking a dorsal spine, and with lateral margins gently convex. Body lacking squamation.

Remarks

The genus *Ctenurella* is distinguished from *Rhynchodus*, *Rhamphodopsis*, *Ptyctodopsis*, *Tollodus* and *Campbellodus* by its absence of a spinal plate. *Chelyophorus* differs in having grooves developed for the external sensory-line system, a shorter, broader nuchal plate and higher, shorter anterior dorsolateral plate. *Austroptyctodus* n.g. is distinguished by its skull-roof pattern, with nuchal plate opened, posteriorly, the different shape of the median dorsal plate and the presence of body scale cover.

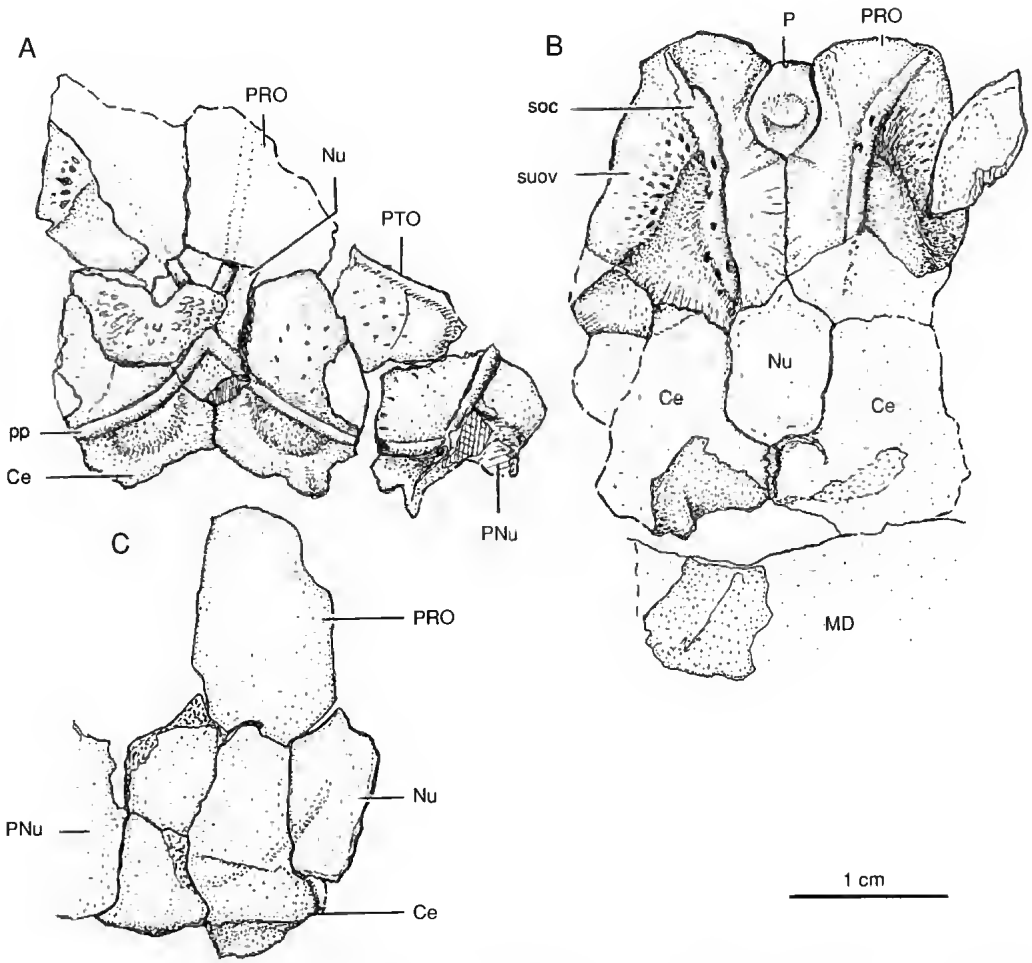

Fig. 24. — *Ctenurella gladbachensis* Ørvig, 1960. Sketches of specimens showing head shield plates in articulated position. **A**, MNHN ARD 233; **B**, MNHN ARD 230b; **C**, MNHN ARD 232. **Ce**, central plate; **MD**, MD1, 2, 3, median dorsal plate(s) or spines; **Nu**, nuchal plate (posterior element), **P**, pineal plate or space provided for it in the head shield; **PNu**, paranuchal plate; **pp**, posterior sensory-line canal on head shield; **PRO**, preorbital plate; **PTO**, postorbital plate; **soc**, supraorbital sensory-line canal; **suov**, supraorbital vault.

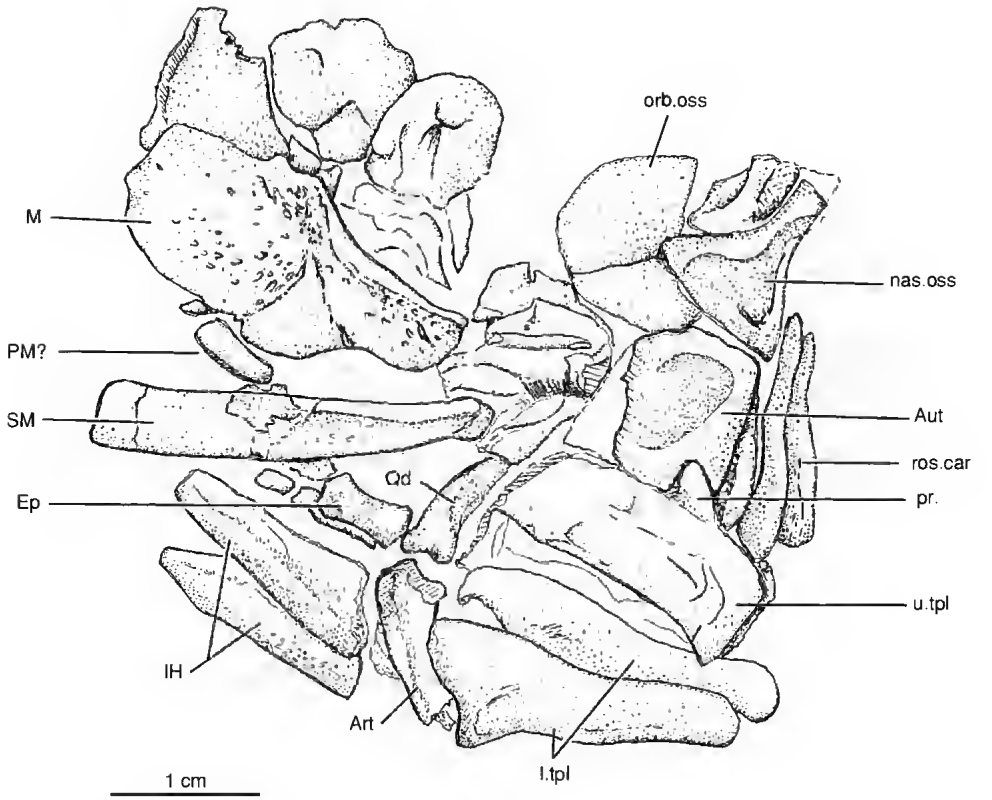

FIG. 25. — *Ctenurella gladbachensis* Ørvig, 1960. Sketch of specimen MNHN ARD 229 (as shown photographed in figure 22). **Art**, articular; **Aut**, autopalatine; **Ep**, epibranchials; **IH**, interhyal element; **l.tpl**, lower tooth plate; **M**, marginal plate; **nas.oss**, nasal ossification of endocranium; **orb.oss**, orbital ossification of endocranium; **PM**, postmarginal plate; **pr.**, dorsal process of the upper tooth plate; **Qd**, quadrate; **ros.car**, rostral cartilages (paired); **SM**, submarginal plate; **u.tpl**, upper tooth plate.

Austroptyctodus gardinieri
(Miles *et* Young, 1977) n.g.
Austroptyctodus n.g.

TYPE SPECIES. — *Austroptyctodus gardineri* Miles *et* Young, 1977.

ETYMOLOGY. — From the continent Australia and the form genus *Ptyctodus*.

DIAGNOSIS. — A ptyctodontid placoderm having a *Ptyctodus*-like crushing dentition, preorbital plates separated from each other by a median gap. Canal-bearing nuchal participating in the posterior margin of the skull roof, trunk shield lacking a spinal plate, median dorsal plate with much wider anterior margin than posterior margin. The body was covered by large overlapping scales.

REMARKS. — *Austroptyctodus* n.g. is clearly distinguished from all other well-known ptyctodontids (*i.e.* those known from most of the dermal armour) except *Ctenurella* and *Chelyophorus*, in lacking a spinal plate. It is distinguished from *Ctenurella* by several features noted above under "Remarks" for *Ctenurella gladbachensis*.

Austroptyctodus gardineri
Miles *et* Young, 1977

Ctenurella gardineri Miles *et* Young, 1977. – Denison 1978: 29. – Long 1984a: fig. 17I-L. – Forey & Gardiner 1986: fig. 2. – Long 1991: 366, fig. 20I, 377.

HOLOTYPE. — WAM 70.4.253, previously described and figured by Miles & Young (1977, pl. 2D, E, pl. 3B, pl. 4B) with the provisional Natural History Museum number for the specimen (P.57637).

OTHER MATERIAL. — NHM, London: P50906,

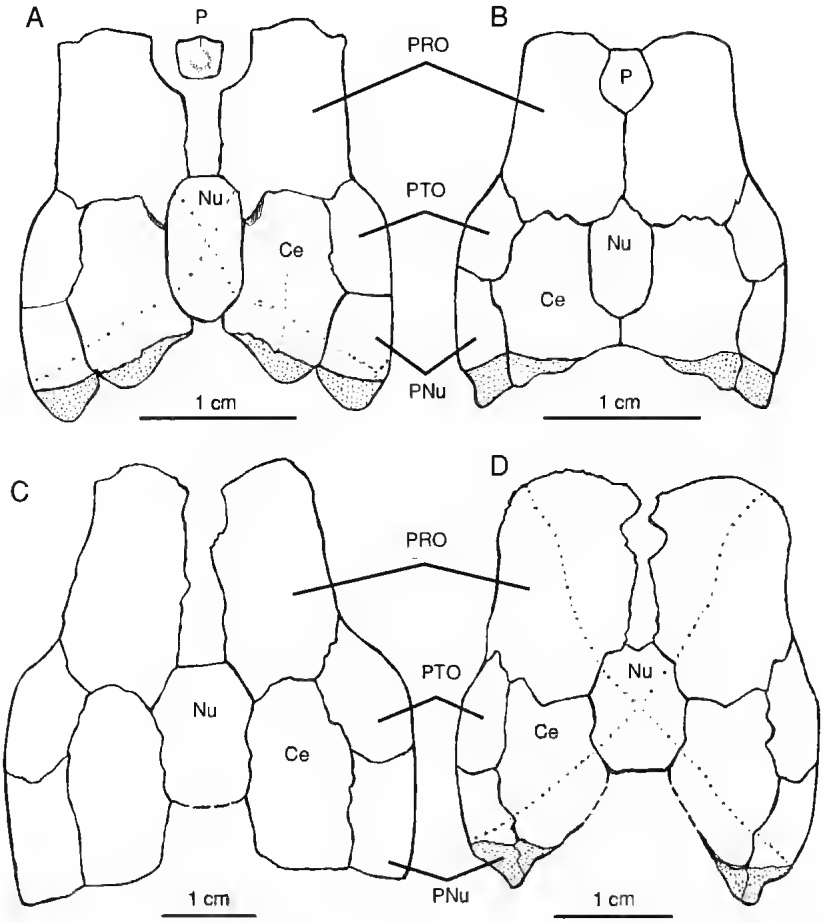

FIG. 26. — Comparison between the reconstructed head shields in dorsal view: **A**, *Austroptyctodus gardineri* (Miles *et* Young, 1977) n.g.; **B**, *Ctenurella gladbachensis* Ørvig, 1960; **C**. *Rhynchodus tetrodon* (after the Holotype); **D**, *Campbellodus decipiens* Miles *et* Young 1977. **Ce**, central plate; **Nu**, nuchal plate (posterior element); **P**, pineal plate, or space provided for it in the head shield; **PNu**, paranuchal plate; **PRO**, preorbital plate; **PTO**, postorbital plate.

P50908, P50909, P50910, P57654, P57655; WAM 86.9.662.

DESCRIPTION

The new Gogo specimen of *Austroptyctodus gardineri* (WAM 86.9.662, Figs 27-29) was collected by the author in August 1986. It is an almost complete specimen preserved as far posteriorly as approximately the middle of the main dorsal fin. It has been prepared by the resin transfer method for both part and counterpart. As Miles & Young (1977) have already described in detail most of the dermal skeleton in this form, the following description focuses only on new information, and provides new reconstructions for the dermal skull roof and visceral skeleton, and external armour in lateral view.

Skull roof and cheek

The skull roof was not reconstructed by Miles & Young (1977, 157) as they stated that "several problems were encountered in attempting to reconstruct the skull-roof from the accurately known shape of individual bones". The new knowledge of the skull roof of *Campbellodus* presented above shows there is not a close fit between all skull roof bones. Earlier, inaccurate reconstructions of the skull roof of *A. gardineri*

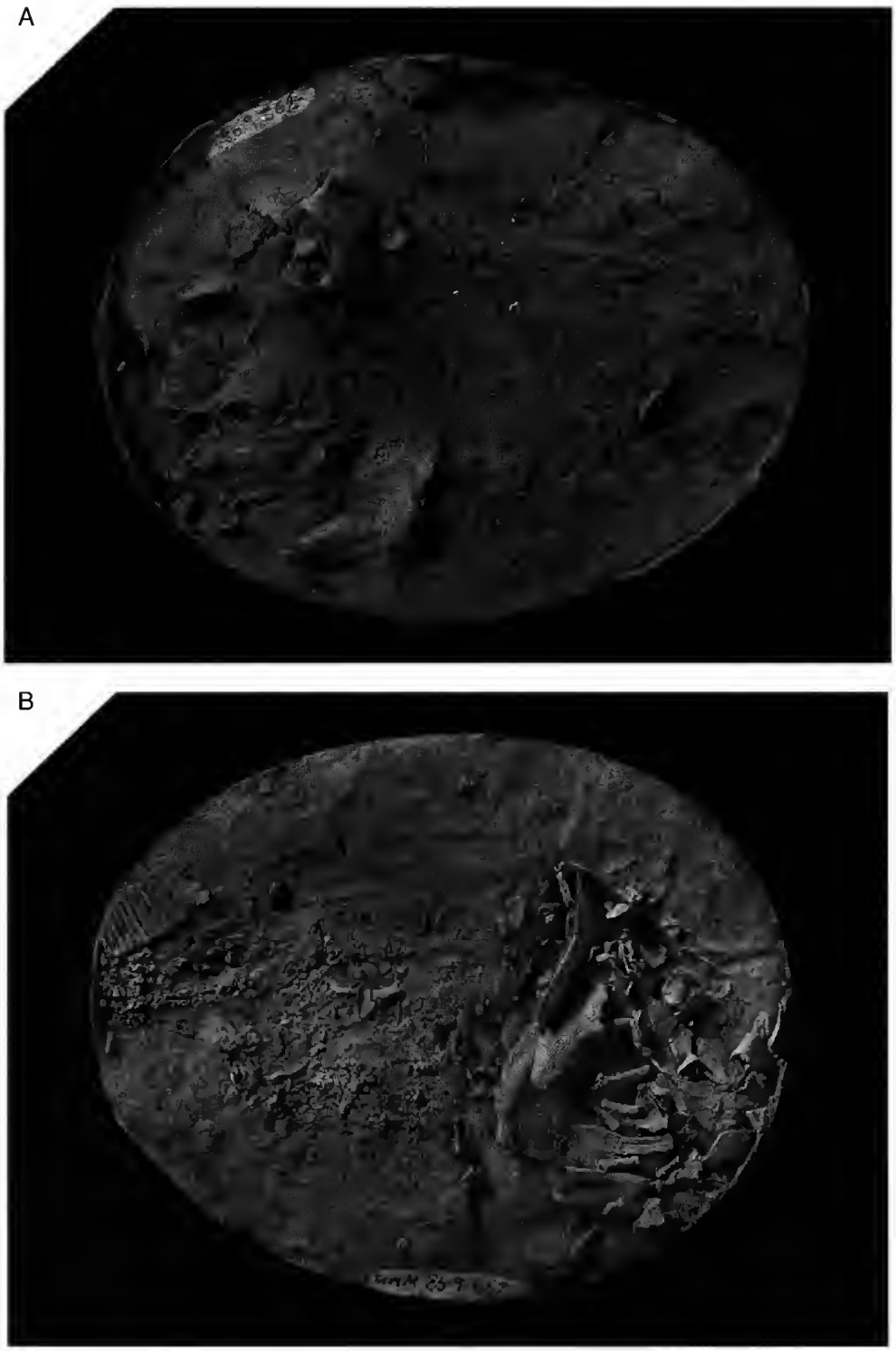

FIG. 27. — *Austroptyctodus gardineri* (Miles et Young, 1977) n.g. WAM 86.9.662, showing both sides of specimen embedded in resin, whitened with ammonium chloride. Natural size.

FIG. 28. — *Austroptyctodus gardineri* (Miles *et* Young, 1977) n.g. WAM 86.9.662, showing details of internal ossifications of the head and part of right side of trunk shield. Whitened with ammonium chloride. See figure 29 for scale.

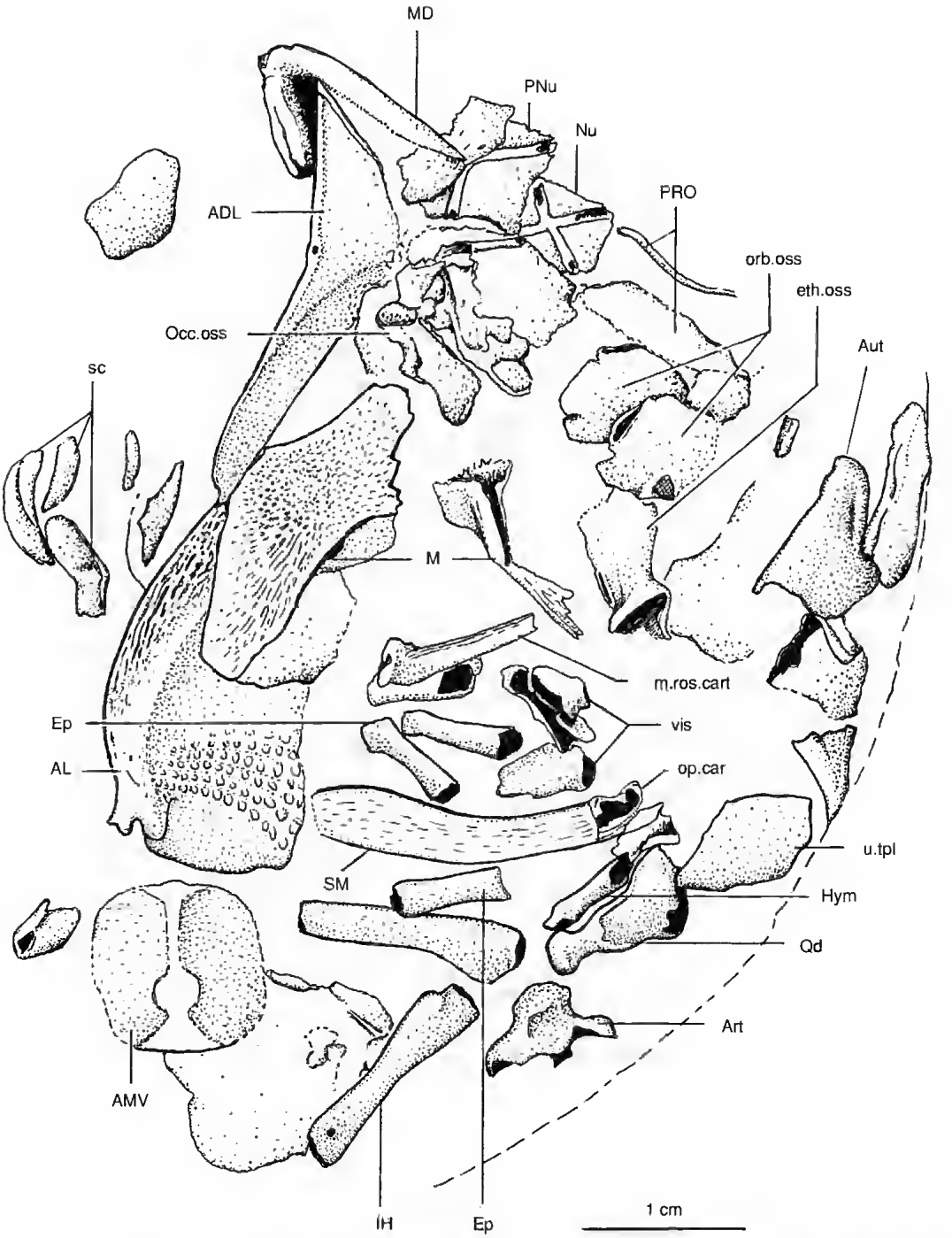

FIG. 29. — *Austroptyctodus gardineri* n.g. (Miles *et* Young, 1977). WAM 86.9.662, sketch interpretation (see figure 27). **ADL**, anterior dorsolateral plate; **AL**, anterior lateral plate; **AMV**, anterior median ventral plate; **Art**, articular; **Aut**, autopalatine; **Ep**, epibranchials; **eth.oss**, ethmoid ossification of endocranium; **Hym**, hyomandibular; **IH**, interhyal element; **M**, marginal plate; **MD**, MD1, 2, 3, median dorsal plate(s) or spines; **m.ros.cart.**, median rostral ossification; **Nu**, nuchal plate (posterior element); **Occ.oss**, occipital ossification of endocranium; **op.car**, opercular cartilage; **orb.oss**, orbital ossification of endocranium; **PNu**, paranuchal plate; **PRO**, preorbital plate; **Qd**, quadrate; **sc**, scales; **SM**, submarginal plate; **u.tpl**, upper tooth plate; **vis**, "visceral skeleton elements?".

were given by Long (1984a, 1991), made by fitting these bones together from sketches. When the bones of one individual are accurately assembled (*e.g.* P57637, WAM 86.9.662), the skull roof closely resembles that of *Campbellodus* in having a median gap between the preorbitals. The pineal plate is actually smaller than the notch as defined for it by the associated preorbital plates (Fig. 26A), as noted by Miles & Young (1977). The visceral surface of the skull roof shows only weak development of the supraorbital vault, without substantial development of an inwardly projecting lamina from the orbital rim, as seen in *Campbellodus*.

The marginal and submarginal plates were well described by Miles & Young (1977). There is no evidence of a smaller postmarginal bone, as suggested to be present in *Ctenurella gardineri* by Ørvig (1970, although this observation is not confirmed by the present study).

Visceral skeleton

As discussed above for *Campbellodus*, the evidence from specimens of *Ctenurella gladbachensis* suggests that the hyoid arch was well-ossified with an expanded interhyal element posteriorly extended to provide an extra attachment region for a flexible opercular membrane. This element was identified as the "ceratohyal" by Forey & Gardiner (1986), and is here shown in various views (Fig. 30). It has two articular heads proximally where it meets the articular and the hyomandibular dorsally (as in *Ctenurella*, Fig. 25). The broad, inwardly curved ceratohyal which is found in *Campbellodus* has not been positively identified in the *Austroptyctodus* material. It was probably not preserved in WAM 86.9.662 as the anterior region of the head is missing, including the lower tooth plates.

Opercular cartilage and hyomandibular. (op.car; Fig. 29) It is found on the inside of the head of the submarginal as in all other placoderms where it is preserved (see Young 1986, for a review of the distribution of this structure). This structure was identified in *Austroptyctodus* by Forey & Gardiner (1986, fig. 1B) as the hyomandibular, and restored as having an enclosed, tubular head. In *Campbellodus*, the corresponding ossification is broader, with an extensive ventral lamina. There is no evidence that it was an elongate element, and a large cartilage structure that acted as the flexible gill-cover has been restored (Fig. 6). WAM 86.9.662 gives further support for interpreting this as an opercular cartilage rather than as an epihyal, as the hyomandibular is seen *in situ*, lying immediately dorsal to the quadrate (Hym; Figs 28, 29). The proximal head of the hyomandibular is not preserved but it terminates in close proximity ventral to the opercular cartilage, presumably meeting the anterior postorbital process of the braincase (a perichondral shell inside the marginal plate), just forward of the centre of the orbital cavity, as it does in *Brindabellaspis* (Young 1980).

Endocranium

Endocranial ossifications in ptyctodontids were first noted by Eichwald (1859, pl. 57, fig. 1) in a well-preserved specimen of *Chelyophorus verneuili*, in which two pairs of roughly circular ossifications were found in the articulated head, below the occipital region and underneath the orbits. This specimen has now been acid prepared to confirm the placement of these ossifications (Dr. A. Ivanov, pers. comm. 1995). Ørvig (1962, 1971) observed perichondrally ossified laminae in the orbitals regions of the Bergisch-Gladbach *Ctenurella* specimens, and Miles (1967: 105a) confirmed the presence of a small semi-circular bone in the orbital region of *Rhamphodopsis*, previously alluded to by Watson (1938).

Miles & Young (1977) gave the first detailed description of the endocranial components of ptyctodontids based on the Gogo specimens of *Austroptyctodus*. They identified at least three pairs of perichondrally-ossified bones which they termed (1) the occipital ossification, (2) the orbital ossification, and (3) the ethmoid ossification. Although various foramina were described on these ossifications, their outlines were not completely clear and so they were only given approximate correlations with the landmark foramina known on the braincases of other placoderms. They further stated that the exact arrangement and relationship of these endocranial ossifications within the articulated head were not clear at all. The new specimen described here gives more precise information on the morphology,

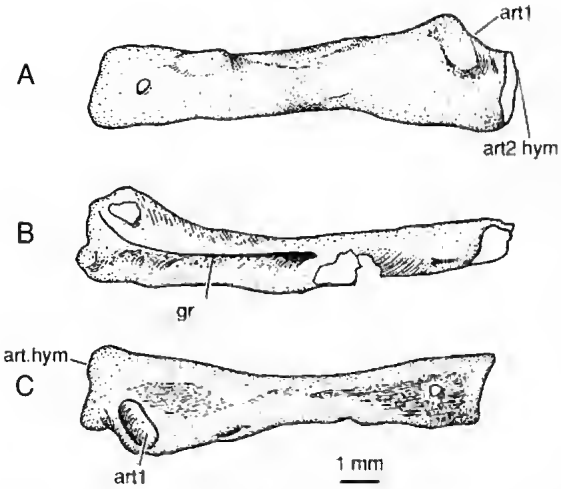

FIG. 30. — *Austroptyctodus gardineri* (Miles *et* Young, 1977) n.g. WAM 86.9.662, right interhyal bone; **A**, **C**, lateral views; **B**, dorsal view. **art**, articulation facets for hyomandibular; **art.hym**, articulation for hyomandibular; **gr**, groove.

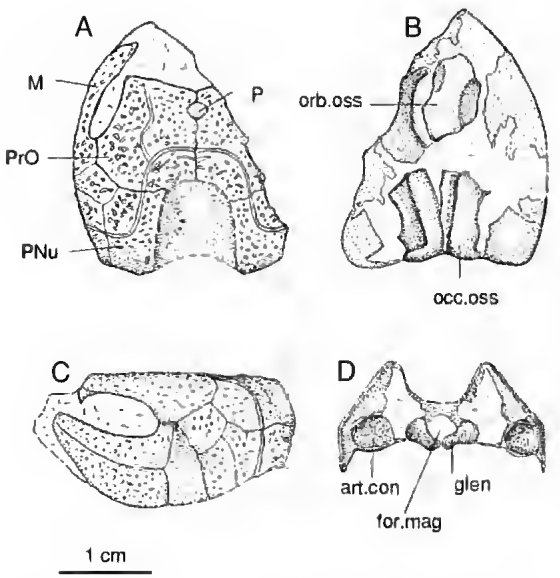

FIG. 31. — *Chelyophorus verneuili* Agassiz, 1844. Articulated specimen, redawn after plate 57, fig. 1 of Eichwald (1859). **A**, head shield in dorsal view; **B**, head in ventral view showing orbital and occipital ossifications of braincase; **C**, head shield in left lateral view; **D**, posterior view of head showing glenoid condyles of braincase and articular flange of paranuchal plates. **art.con**, articular condyle or face on ADL plate; **for.mag**, foramen magnum of endocranium; **glen**, glenoid condyle of endocranium; **M**, marginal plate, **occ.oss**, occipital ossification of endocranium; **orb.oss**, orbital ossification of endocranium; **P**, pineal plate or space provided for it in the head shield; **PNu**, paranuchal plate; **PrO**, preorbital plate.

position and contact relationships of these elements and can be corroborated by new observations on the endocranial ossifications examined in both *Chelyophorus verneuili* and *Ctenurella gladbachensis*. Recently prepared material of a new genus of ptyctodontid from the Late Devonian Gneudna Formation of Western Australia also shows the occipital and orbital ossifications perfectly preserved in 3-dimensional form, corroborating the foramina and morphological features with those preserved in other ptyctodontids.

Three paired ossifications of the endocranium of *Austroptyctodus* are preserved in WAM 86.9.662 (occ.oss, orb.oss, eth.oss; Figs 28, 29), all in close association and only displaced slightly from articulated position, as supported by the close articulation of the other neighbouring dermal bones. A fourth pair of bones lies dorsal to the palatoquadrate which precede the nasal capsules. These have been labelled as "metapterygoids" in previous descriptions. There are also perichondral conical shells of bone attached to the inside wall of the marginal plate that contacted the orbital ossifications laterally. These are here assumed to have housed the posterior postorbital process, as for other placoderms (Young 1979, 1980, 1986; Lelievre 1995).

The presumed position of the posterior three of these paired endocranial ossifications, with relation to the dermal exocranium, was proposed by Miles & Young (1977, fig. 22) who correctly positioned the occipital bones but restored the orbitals as oriented with their flat lamina vertically. They did not attempt to place the ethmoid ossification in relation to the skull roof, but noted that its large anterior articulation facet was most likely an articulation to the autopalatine, as also pointed out by Young (1986). Evidence from the new specimen (Fig. 28) shows an alignment of the occipital, orbital and ethmoid bones, each part only slightly displaced from its antimere. The assumed fit of these bones is in line forming the ventral wall of the endocranium, as shown by *Chelyophorus verneuili* (Fig. 31, redrawn from Eichwald 1859) and in several specimens of *Ctenurella gladbachensis* in which the paired orbital ossifications remain articulated mesially, usually found in close proximity to the

orbits (as it also occurs in the holotype of *Austroptyctodus*, WAM 70.4.253). Other specimens of this species show the ethmoid articulation in the anteroventral corner of the orbit, closely associated with the autopalatine and metapterygoid, and with the head of the submarginal bone snuggled into a depression immediately behind its large articulatory facet. Thus, from these various specimens it is now possible to redescribe and accurately reconstruct the endocranium in *Austroptyctodus*, and to discuss the homology of parts of its structure to that in other placoderms.

Occipital ossification

The occipital ossification was well described by Miles & Young (1977, fig. 20), although the margins of their specimen were not well-preserved enough to show its complete shape. In *Austroptyctodus* (WAM 86.9.662), as well as in *Chelyophorus* and in the new Gneudna ptyctodontid, the occipital ossifications are well-preserved and show their complete outlines. The material largely supports the reconstructions of Miles & Young (1977), showing that the ventral lamina of this bone possessed a large groove (gr, dla; Fig. 32C) that presumably carried the dorsolateral aorta, with each side carrying the groove anterolaterally away from the glenoid condyles. In lateral view (Fig. 32A), there are three large foramina visible and the outer damaged part of the ascending occipital process (pr.oc; Fig. 32 A) reveals that there was a hollow tube in the outer wall of the ossification, probably opening in the position where Miles & Young (1977, fig. 20C) observed a slit in the endocranial wall. The anterior two of these large foramina in the lateral wall of the occipital ossification (Fig. 32A, B, for 2, 3) were tentatively identified as for the vagus and glossopharnygeal netves by Miles & Young. This interpretation would seem correct by comparison with the foramina found in the similar region of lateral endocranial wall occupied by other known placoderms (e.g. *Brindabellaspis*, Young 1980; *Dicksonosteus*, Goujet 1984a; *Macropetalichthys*, as reinterpreted by Young 1986). There is also a large ventral slit containing a foramen lateral to the glenoid process (Fig. 32A, for), also recognised by Miles & Young (1977, fig. 20, c1, sl). As this opening is posteriorly directed and not confluent with the pathway for the dorsolateral aorta, it may possibly represent the path of the occipital

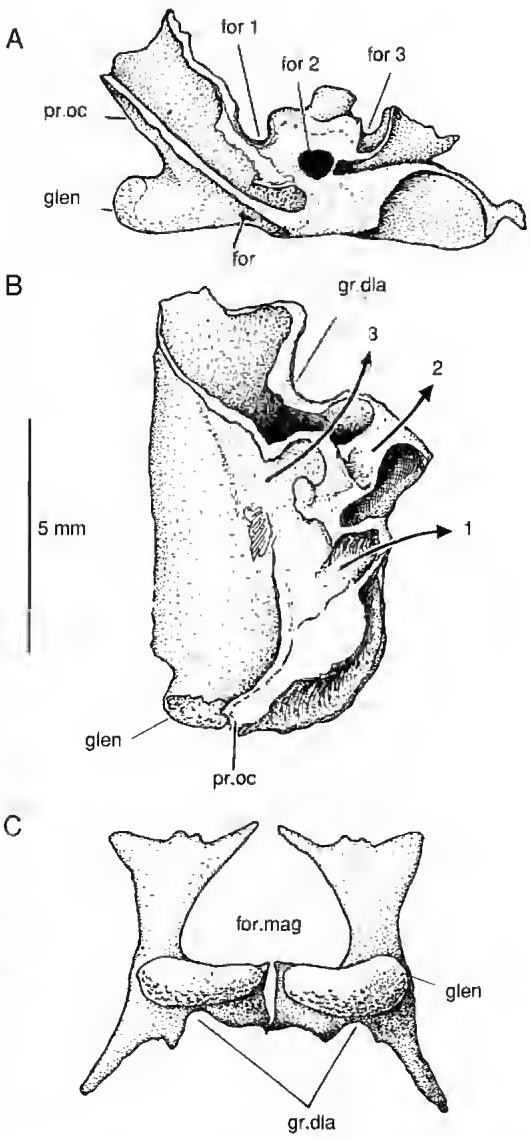

FIG. 32. — *Austroptyctodus gardineri* (Miles et Young, 1977) n.g. WAM 86.9.662. **A**, **B**, right occipital ossification of braincase; **A**, mesial view; **B**, lateral view. **C**, reconstruction of posterior view of braincase. **for**, for 1, 2, 3, foramen or identified series of foramina; **for.mag**, foramen magnum of endocranium; **glen**, glenoid condyle of endocranium; **gr.dla**, groove for one branch of the dorsolateral aorta; **pr.oc**, ascending occipital process of braincase.

artery (also located in this position in *Brindabellaspis*, Young 1980, figs 7, 8).

Orbital ossification

The orbital ossification figured by Miles & Young (1977) was interpreted on the basis of its presumed orientation. They restored it as lying vertically behind the orbital cavity based on one specimen (P50908), with the structure interpreted as the attachment for an eyestalk located far posterior of the eyeball. The foramina for transmitting vessels or nerves were thus seen passing from within the braincase to the orbital cavity. Specimens of *Ctenurella gladbachensis* show that the orbital ossifications are always joined mesially and lie within the orbit, implying that they may have been positioned horizontally in life, thus forming the ventral wall of the orbital cavity. This interpretation is further supported by Eichwald's (1859) figured articulated specimen of *Chelyophorus verneuili*, which shows in ventral view the paired occipital ossifications *in situ* (Fig. 31), with one of the paired orbital ossifications laying just anterior to these. An excellent specimen of an orbital ossification of *Chelyophorus verneuili* in the MNHN collections has been freed from the matrix and is figured here alongside those of the *Austroptyctodus* specimens (Fig. 33C, D) to illustrate further the morphology of this bone. Additional evidence for the horizontal position of the orbital ossification is provided by the extensive mesial lamina of the marginal plate in both Gogo ptyctodontids, in which an extensive dorsal lamina is developed, and which still bears its connection to the orbital ossification in the holotype specimen of *Austroptyctodus gardineri*.

I have restored the orbital ossifications as being oriented transversely and longitudinally below the orbit, in mesial contact with each other, connected by cartilage to the dorsal, mesially directed shelf above the perichondral cone, for the posterior postorbital process of the endocranium (Fig. 34). This is based on several pieces of evidence:

1. Their position in the articulated specimen WAM 86.9.662 (orb.oss; Figs 28, 29) in which the paired orbital ossifications lay very close to each other, a short distance anterior to the paired occipital ossifications (seen in ventral view) and in close proximity to the ethmoid ossification.

2. In the holotype of *Austroptyctodus gardineri* the orbital ossification is articulated with the mesial perichondral process of the marginal plate, suggesting horizontal aligment as the mesial lamina of the marginal is horizontal in life position.

3. The fact that they are joined mesially in some specimens of *Ctenurella gladbachensis*.

4. The fact that the articulated, uncrushed specimen of *Chelyophorus verneuili* shows the horizontal position of the orbital ossifications in continuity with the horizontal laminae of the occipital ossifications (see Fig. 31).

The orbital ossifications are seen to lie in the transverse plane forming the central division of the ventral endocranial wall, most of which forms the extensive subocular shelf. The dorsally elevated process on the lateral margin of the orbital ossification is most likely an eyestalk attachment, situated more to the anteromesial part of the orbit, as it is in other placoderms (e.g. *Buchanosteus*, *Brindabellaspis*, Young 1986).

A large robust articulation, lying to the anterolateral corner of the orbital ossification, can be interpreted as a strong cartilaginous connection to the perichondral, thickening on the visceral surface of the marginal plate, thus bracing the lateral wall of the endocranium with the marginal plate. In this respect it is most possibly an homologue of the posterior postorbital process of other placoderms, which abuts the marginal plate in arthrodires (*Buchanosteus*, Young 1979). It appears to be too posteriorly situated either for the opercular cartilage or for hyomandibular articulation to the braincase, which are located adjacent to the ethmoid ossification and can be seen by the anterior position of the head of the submarginal plate with respect to the orbit on articulated specimens of both *Ctenurella gladbachensis* and *Austroptyctodus gardineri*.

The two foramina piercing the orbital ossification are small in comparison with those for the major nerves in placoderms, and do not pass from the brain cavity, but from the ventral surface of the endocranium into the orbital region. These foramina are clearly seen in the isolated orbital ossification of *Chelyophorus verneuili* (Fig. 33C, D) but they are so small in the Gogo specimen that they tend to be obscured by the

consolidating glue and are seen as depressions (Fig. 33). Thus, only one large canal is seen penetrating the bone near the eyestalk attachment in the Gogo specimen, and this is possibly the canal for the orbital artery (orb.a; Fig. 33). A larger canal more posteriorly situated on the orbital ossification of *Chelyophorus*, emerging from a well-defined pit on the dorsal surface (orbital cavity), is most likely for the internal carotid artery emerging from the ventral myodome (i.car, v.my; Fig. 33C, D) which in *Dicksonosteus* (Goujet 1984a) and *Brindabellaspis* (Young 1980) runs up through the subocular shelf and into the ventral myodome for the eye muscles. Other smaller foramina which do not seem to penetrate through the ossification may be vascular supply canals for the interperichondrium.

There are two well defined notches embayed into the lateral margins of the orbital ossifications in

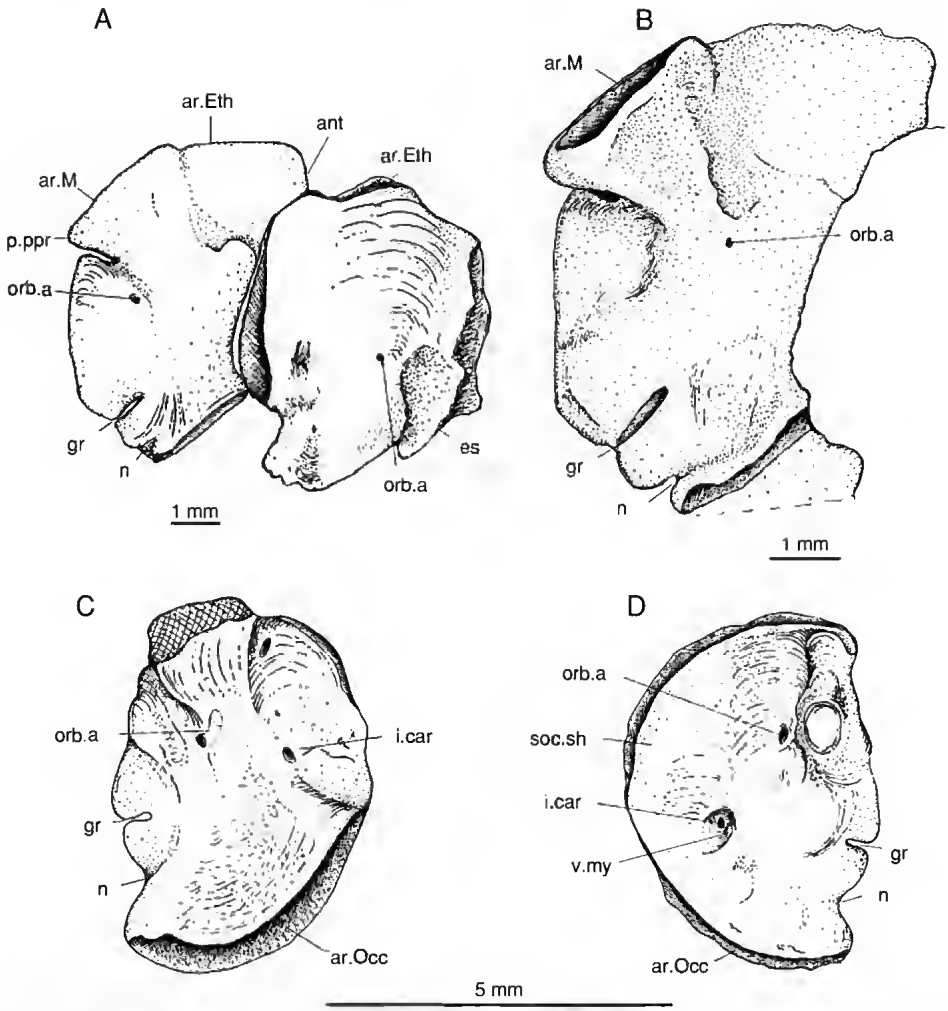

FIG. 33. — *Austroptyctodus gardineri* n.g. (Miles et Young, 1977). WAM 86.9.662, orbital ossifications of braincase. **A**, paired units as preserved (see figures 27, 28 for position with respect to rest of specimen); **B**, detail of left orbital ossification in ventral view. **C**, **D**, *Chelyophorus verneuili* Agassiz, 1844, MNHN specimen, Agassiz type collection (unnumbered, Collection of Verneuil, Laboratoire de Paléontologie, MNHN): left orbital ossification; **C**, ventral view; **D**, dorsal view. **ant**, anterior direction; **ar.Eth**, articulation for ethmoid ossification; **ar.M**, articulation for marginal plate; **ar.Occ**, articulation for occipital ossification; **es**, eyestalk attachment; **gr**, groove; **i.car**, internal carotid foramen; **n**, notch; **orb.a**, foramen for orbital artery; **p.ppr**, possible homologue of the posterior postorbital process of endocranium; **soc.sh**, subocular shelf; **v.my**, ventral myodome.

both *Gogoptyctodus* and *Chelyophorus* (gr, n; Fig. 33). As these are considerably larger than the arterial foramina, the largest of these, situated posterior to the eyestalk and internal carotid foramen, is possibly for the pituitary vein.

Ethmoid ossification

The ethmoid ossification has been well-described by Miles & Young (1977), but was not restored in relation to the rest of the endocranium and jaw suspensory mechanism. The new material adds nothing new to the description of the ethmoid ossification, as no isolated ethmoid ossifications have yet been recovered from the Russian material or the new Gneudna specimens. It should be noted that Ørvig (1962) restored the ethmoid ossification in *C. gladbachensis* with a large anteriorly facing articulatory facet for the palatoquadrate, and labelled it as the "metapterygoid". It seems likely that the large anterior facets on the ethmoid faced anterolaterally, as suggested by Miles & Young, to articulate with the articulatory facets on the autopalatine, the midlines of the ethmoid ossifications meeting medially held by cartilage.

Nasal ossification

Observation of the Bergisch-Gladbach material of *Ctenurella gladbachensis* and of *Austroptyctodus gardineri* shows that the ethmoid ossification is always preserved in a position ventral to the "metapterygoids" of the palatoquadrate. In the holotype of *Austroptyctodus* (Miles & Young 1977; Fig. 23) the right "metapterygoid" is separated from the autopalatine and rests immediately dorsal to the ethmoid ossification, which clearly separates this ossification from the upper jaw ossifications. This leads me to propose that the "metapterygoid" has been misinterpreted and is actually not part of the upper jaw apparatus but could represent a paired nasal ossification partly enclosing the nasal capsules. These bones sit anterior to the orbits directly dorsal to the upper jaw ossifications (nas.oss; Fig. 35), in a position appropriate for the external nares by comparison with other placoderms. The shape of the ossification as described for *Austroptyctodus* by Miles & Young (1977, fig. 26) shows that the lateral face is concave and would have been able to support the olfactory bulb, in a way similar to the preorbital recess of antiarchs, immediately anterior to the orbit. The presence of paired nasal ossifications is known in arthrodires as cribrosal bones, clearly seen in many of the Gogo eubrachythoracids (e.g. *Eastmanosteus*, Dennis-Bryan 1987; *Latocamurus*, Long 1988c; plourdosteids, see Gardiner & Miles 1990). There is a groove and a ridge developed on the mesial side of the bone, noted by Miles & Young (1977: 176) as possibly being for attachment to the endocranium. The well-defined groove which runs dorsally and anteriorly above the cavity for the nasal capsule is possibly for a terminalis nerve, which has been identified mesial to the nasal capsules in the arthrodire *Latocamurus* (Long 1988c). The nasal ossifications had well-developed posterodorsal processes (Miles & Young 1977, "prmpt" fig. 26) which may have mesially been joined by ligaments. The function of this unusual process on the nasal ossifications could have been as an attachment region for the median rostral cartilage (m.ros.cart; Fig. 28), an ossification present in some ptyctodontids but absent in all other placoderms.

Reconstruction of the endocranium

A reconstruction of the endocranium in ptyctodontids was given by Miles & Young (1977, fig. 22) based on the available specimens of *Austroptyctodus gardineri*. In light of the new material and the evidence from new observations on the articulated position of braincase ossifications in both *Chelyophorus* and *Ctenurella*, it is now possible to provide a new sketch reconstruction of the ptyctodontid endocranium (Fig. 34). The position of the occipital ossifications is clear as the glenoid processes are always aligned with horizontal long axes, as correctly restored by Miles & Young (1977, fig. 22B, and shown here Fig. 32C), as it also occurs in the articulated specimen of *Chelyophorus* (Fig. 31). That the paired orbital ossifications lie in the horizontal plane below the orbit has been argued above from evidence seen in uncrushed articulated specimen of *Chelyophorus*, plus observations on the Gogo and Bergisch-Gladbach specimens. The relative sizes of the occipital, orbital, ethmoid and nasal ossifications in relation to the skull roof are clearly seen from WAM 96.9.662, upon which the dor-

sal view outline reconstruction of the endocranium was largely based. The position of the ethmoid ossifications immediately anterior to the orbital ossifications and articulating with the palatoquadrate is also based on observations of *Ctenurella* and of the WAM 86.9.662 specimen of *Austroptyctodus*. Finally, the position of the paired nasal ossifications, anterior to the ethmoid ossifications and sitting above the palatoquadrate and behind the inferred position of the nares, is a new interpretation based on observations of several specimens of articulated *Ctenurella* and *Austroptyctodus*.

The braincase of ptyctodontids, as restored herein, is unique amongst placoderms in comprising at least four paired perichondral components, forming a solid floor to the endocranium but lacking any dorsal ossification. Furthermore it is unlike any other placoderm in having a median suture running down its midline where opposite sides of the paired ossifications are joined by cartilage. The rounded shape of the orbital ossifications implies that a space exists anterior to the mesial connection betwen these units and the ethmoid ossifications immediately anterior to them. This could be for a ventral hypophysial

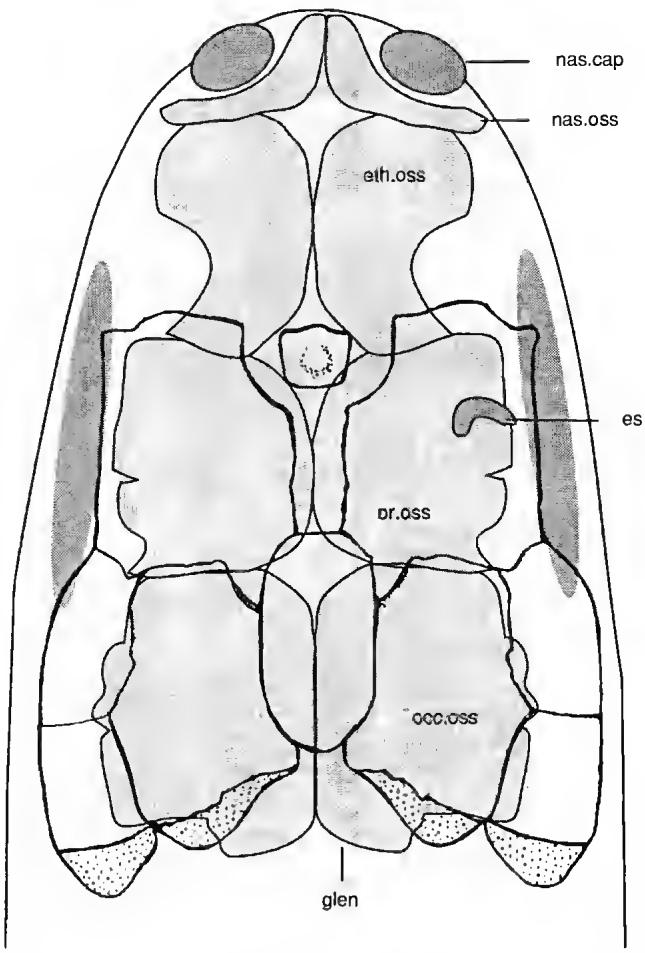

FIG. 34. — Attempted reconstruction of the endocranium in dorsal view (shaded) of *Austroptyctodus gardineri* (Miles *et* Young, 1977) n.g., based largely on WAM 86.9.662. Outline of skull roof bones shown as transparent. **es**, eyestalk attachment; **eth.oss**, ethmoid ossification of endocranium; **glen**, glenoid condyle of endocranium; **nas.cap**, nasal capsule; **nas.oss**, nasal ossification of endocranium; **occ.oss**, occipital ossification of endocranium; **or.oss**, orbital ossification of endocranium.

opening. There is no parasphenoid ossification as in arthrodires, phyllolepids and in the acanthothoracid *Kosoraspis*.

Figure 35 provides a revised reconstruction for the dermal exoskeleton and visceral skeleton, as known for *Austroptyctodus gardineri*.

Dermal scales

Thin scales covered the tail of *Austroptyctodus gardineri*, as preserved in WAM 86.9.662 (sc; Figs 27-29). They closely resemble those of *Campbellodus* in overall form, being boomerang-shaped, much higher than long in the articulated squamation, with a dorsal external lamina and a ventral overlapped region. The external ornamentation is a very fine reticulate pattern.

SUMMARY AND CONCLUSIONS

1. The genus *Campbellodus decipens* Miles *et* Young is redescribed from a complete new specimen, showing it to have three median dorsal plates, a dermal scale cover and well-ossified anterior gill arch series. The skull roof shows that the preorbitals plates did not suture in the midline, as it is now known to occur in some other

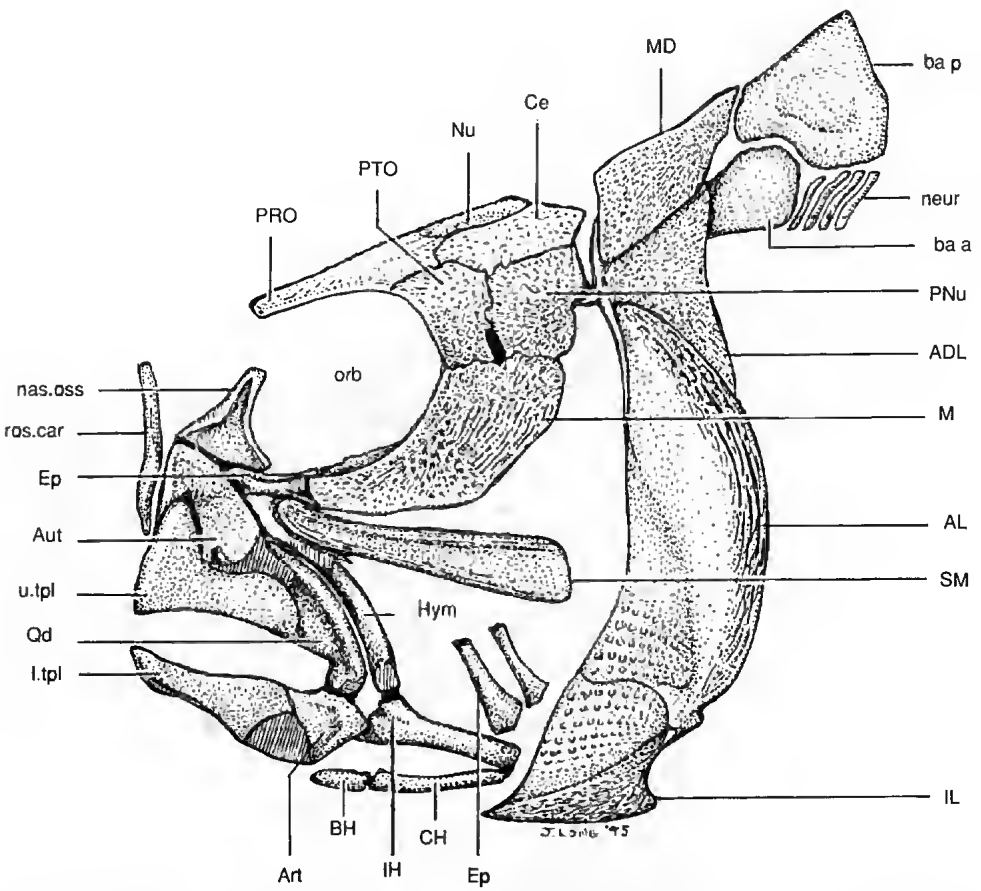

Fig. 35. — Attempted reconstruction of the dermal exoskeleton and visceral endoskelton of *Austroptyctodus gardineri* n.g. (Miles *et* Young, 1977), based largely on WAM 86.9.662 and on the holotype, WAM 70.4.253. **ADL**, anterior dorsolateral plate; **AL**, anterior lateral plate; **Art**, articular; **Aut**, Autopalatine; **ba a**, **ba p**, anterior and posterior basals plates; **BH**, basihyal; **Ce**, central plate; **CH**, ceratohyal; **Ep**, epibranchials; **Hym**, hyomandibular; **IH**, interhyal element; **IL**, interolateral plate; **l.tpl**, lower tooth plate; **M**, marginal plate; **MD**, MD1, 2, 3, median dorsal plate(s) or spines; **nas.oss**, nasal ossification of endocranium; **neur**, neurals arches; **Nu**, nuchal plate (posterior element); **orb**, orbit; **PNu**, paranuchal plate; **PRO**, preorbital plate; **PTO**, postorbital plate; **Qd**, quadrate; **ros.car**, rostral cartilages (paired); **SM**, submarginal plate; **u.tpl**, upper tooth plate.

ptyctodontids (e.g. *Austroptyctodus* n.g., *Rhynchodus tetradon*).

2. The large, posteroventrally directed gill arch bones that lie immediately behind the jaw articulation in ptyctodontids had previously been interpreted as "ceratohyals" in *Ctenurella* and in the Gogo form *Austroptyctodus*. New evidence from *Campbellodus* and *Austroptyctodus* n.g. suggests that these are modified interhyal elements and that the ceratohyals are large, deep bones, as occur in *Campbellodus*.

3. Revision of some Bergisch-Gladbach specimens of *Ctenurella gladbachensis* Ørvig, 1960 shows that the skull roof had been incorrectly restored, and that the centrals do in fact meet each other behind the nuchal plate. A revised diagnosis of the genus is given.

4. "*Ctenurella*" *gardineri* Miles *et* Young, 1977 is shown to differ from *Ctenurella gladbachensis* in the arrangement of skull roof bones and body squamation, and is here referred to a new genus, *Austroptyctodus gardineri* n.g.

5. The braincase in ptyctodontids is interpreted to comprise at least four paired perichondral ossifications, the occipital, orbital, ethmoid and nasal units. The latter was previously identified as being the "metapterygoid". Perichondral units attached to the inside of the marginal plate may have housed the posterior postorbital process of the endocranium, as in other placoderms. Ptyctodontids apparently lacked a parasphenoid.

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Evolution of the premaxillary in the primitive fossil actinopterygians

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ABSTRACT
The different conditions of the premaxillary in primitive actinopterygians are individualized, or fused to adjacent bones. Their dental field can also be divided and fused to neighbouring bones, the premaxillaries may be separated across the midline, or, finally, they have disappeared. This separation and absence can result in a rostral notch observed in rhadinichthyids, and presumed in other groups such as the redfieldiiformes. It can be suggested that the plesiomorphous gnathostome dermal skeletal condition is mictomeric, that the primitive actinopterygian larval snout condition derived from that condition was mesomeric, and that heterochronic changes during early actinopterygian evolution gave rise during development (1) of mesomeric adult primitive actinopterygians through neoteny, (2) of macromeric adult primitive actinopterygians through fusions of bones, (3) to the condition of actinopterygians lacking a premaxillary through its loss. The neopterygian condition may have arisen through paedomorphosis from either mesomeric primitive fossil actinopterygians, or directly by heterochrony from the larval primitive condition.

KEY WORDS
Vertebrata,
Actinopterygii,
comparative anatomy,
evolutionary trend,
premaxillary,
dermal snout.

RÉSUMÉ

Les différentes dispositions du prémaxillaire chez les actinoptérygiens primitifs sont : différencié ou fusionné à des os adjacents, le territoire dentaire peut être divisé et fusionné à des os voisins, les deux prémaxillaires être séparés sans contact l'un avec l'autre, enfin le prémaxillaire peut avoir disparu. Cette séparation ou cette absence se traduisent le plus souvent par une lacune osseuse rostrale observée chez des rhadinichthyidés et supposée dans plusieurs autres groupes dont les redfieldiiformes. Il est suggéré que la disposition plésiomorphe du squelette dermique des gnathostomes est micromérique, que la disposition larvaire du museau des actinoptérygiens dérivée de cette disposition plésiomorphe était mésomérique et que les changements hétérochroniques au début de l'évolution des actinoptérygiens ont donné pendant le développement, (1) par néoténie, des actinoptérygiens primitifs adultes mésomériques, (2) par des fusions osseuses, des actinoptérygiens primitifs adultes macromériques, (3) par disparition, des formes dépourvues de prémaxillaire. Les néoptérygiens seraient issus par pédomorphose, soit des actinoptétygiens primitifs fossiles mésomériques, soit directement, par hétérochronie de la disposition primitive larvaire.

MOTS CLÉS
Vertebrata, Actinopterygii, anatomie comparée, tendance évolutive, prémaxillaire, museau dermique.

INTRODUCTION

The snout in teleostome fishes is a region of the dermal skull concentrating elements sensitive to adaptations and evolution, as it bears teeth, narial openings and the anteriormost part of the lateral sensory system. The variations of its anatomy have been often dealt with in the past (Westoll 1937; Pehrson 1947, 1958; Gardiner 1963; Wenz 1967; Pearson & Westoll 1972; Patterson 1975; Pearson 1982; Schaeffer 1984; Long 1988). More recently the evolutionary implications of some of its bony units in lower actinopterygians were discussed (Poplin & Lund 1995). In the present work, analysis is focussed on the area of the premaxillary among the dermal bones of the snout which underwent the most numerous modifications of any area of skull bones. Therefore, it is potentially one of the most significant complexes of bones and lateral line canals for phylogenetic purposes in lower actinopterygians. Because of difficulties in observation and preservation in fossil fishes, accurate descriptions and reconstructions of the snout are rather rare so that we refer here to the best known taxa, even if reappraisials of them should be eventually desirable.

THE DIFFERENT STATES OF THE PREMAXILLARY IN LOWER ACTINOPTERYGIANS

In order to avoid confusion owing to the many bone nomenclatures used by authors, which somehow darkened the understanding of the dermal snout evolution in the past, the "premaxillary" is defined here as the most anterior paired upper anamestic toothbearing bone of the rim of the mouth. When it is fused to other bony territories, compound names are used (Poplin & Lund 1995). As a whole, the five following states of the premaxillary have been observed among primitive actinopterygians.

1. Individualized typical premaxillae are rather rare in lower fossil actinopterygians: for instance, in Lower Carboniferous, fishes from Bear Gulch (Montana, USA), the Triassic *Pteronisculus* (Nielsen 1942), *Perleidus* (Fig. 1A; Lehman 1952). According to Hutchinson (1978), it is also present in monophyletic lineages such as the Triassic Brookvaliidae and Schizurichthyidae. In recent forms, separate premaxillaries are present in larval *Polypterus* (Fig. 1B; Pehrson 1947, 1958) and in all the neopterygians, where they

may even be larger than the maxillae (Fig. 1C).

2. More often, in lower fossil actinopterygians, the premaxillary is fused with adjacent bones resulting in compound bony units such as "rostro-premaxillo-antorbitals", "rostro-premaxillaries" and "antorbito-premaxillaries" (Fig. 1D, E; Poplin & Lund 1995). In adult *Polypterus* the

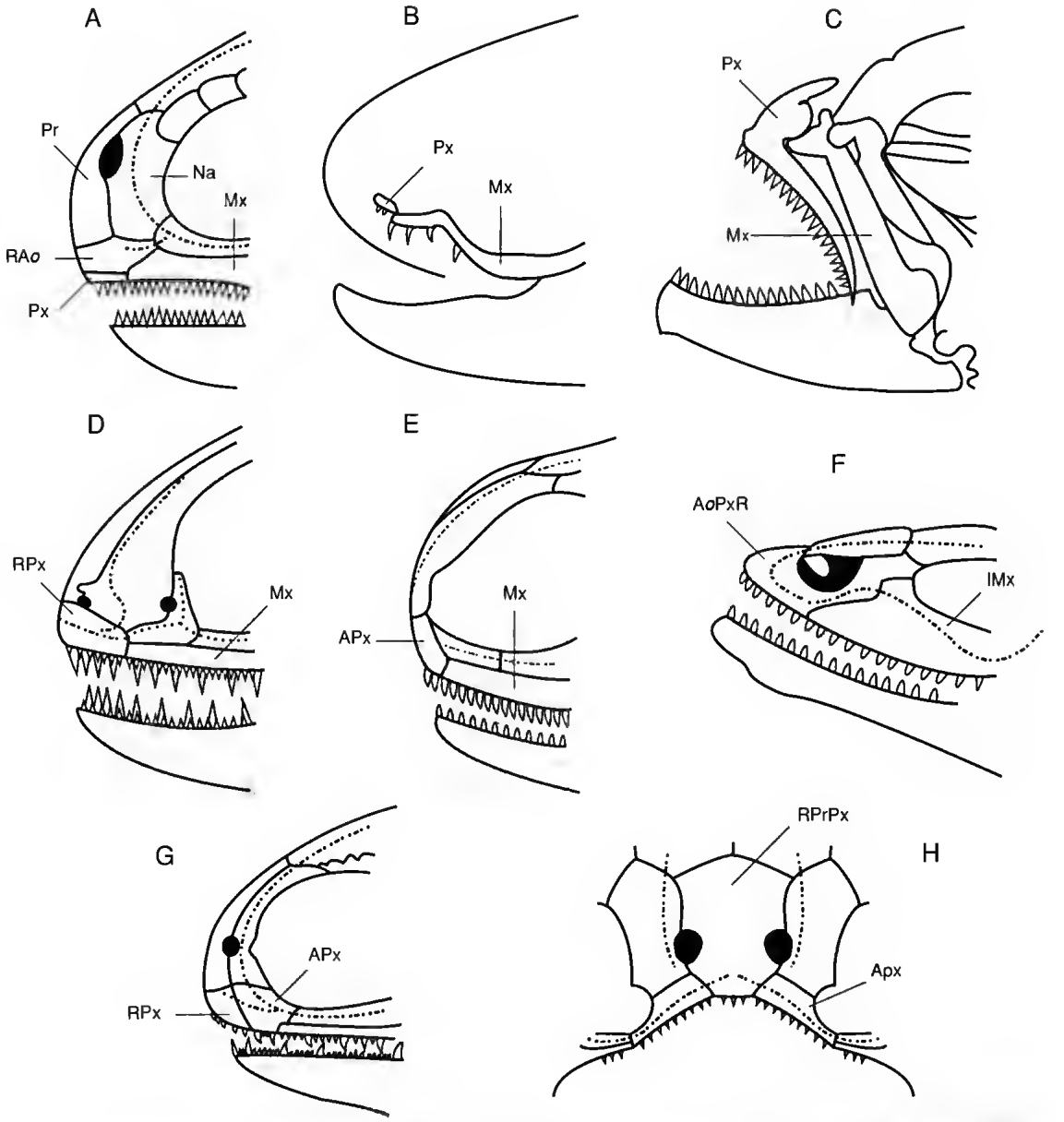

Fig. 1. — Dermal snouts: **A-G**, left lateral view; **H**, front view. **A**, *Perleidus piveteaui* (after Lehman 1952, fig. 86); **B**, *Polypterus*, 9.6 mm larva (after Pehrson 1958, fig. 8); **C**, *Pomatomus saltatrix* (after Gregory 1933, fig. 177); **D**, *Birgeria groenlandica* (after Nielsen 1949, fig. 69); **E**, *Moythomasia nitida* (after Jessen 1968, fig. 1); **F**, *Polypterus* adult (after Daget 1958, fig. 1791); **G**, *Watsonichthys pectinatus* (after Gardiner 1963, fig. 1); **H**, *Howqualepis rostridens* (after Long 1988, fig. 14B). **APx**, antorbito-premaxillary; **AoPxR**, antorbito-premaxillo-rostral; **IMx**, infraorbito-maxillary; **Mx**, maxillary; **Na**, nasal; **Px**, premaxillary; **Pr**, postrostral; **RAo**, rostro-antorbital; **RPx**, rostro-premaxillary; **RPrPx**, rostro-postrostro-premaxillary.

premaxillary is fused to the lateral rostral and to the antorbital (Fig. 1F; Pehrson 1947, 1958; Lehman 1958: 2092).

3. The territory of the premaxillary dental field may also be divided into two units that are fused to neighbouring bones (Moy-Thomas 1934; Ten Cate 1985). This is the case for instance in *Watsonichthys pectinatus* (Fig. 1G) which shows an antorbito-premaxillary together with a rostro-premaxillary. The Devonian *Moythomasia durgaringa* and *Howqualepis rostridens* (*cf.* Gardiner 1984; Long 1988) are more complex and questionable cases (Fig. 1H); their anterior marginal teeth are borne by three bones: paired antorbito-premaxillaries (= Gardiner's and Long's "premaxillaries") and a median rostro-postrostro-premaxillary (= "dentigerous rostro-postrostral"). According to our interpretation, the territories of the right and left premaxillaries (or their dental fields) are divided into four units: the median ones are fused to the single rostro-postrostral and the lateral ones are fused to the paired antorbitals (Poplin & Lund 1995).

4. In some cases, such as in some Bear Gulch taxa, both premaxillaries are so weak and so loose that they are not in contact with each other. This situation results in a small median rostral notch quite like that described below.

5. The last state of the premaxillary is encountered in a number of primitive fossil actinopterygians: its disappearance revealed by the complete absence of the characteristic features of its territory, *i.e.* anamestic and presence of anrerior marginal teeth (Poplin & Lund 1995).

Such a lack has been sometimes observed, or suspected, in the past. Westoll (1937) and later Heyler (1969) noticed that the Aeduellidae have no premaxillaries. The Redfieldiiformes gave rise to a small disagreement on this respect between Hutchinson (1973, 1978) and Schaeffer (1967, 1984): the former thinks that the lack of a premaxillary characterizes only the family Redfieldiidae, and the latter claims that it is a feature of the whole order. More recently the absence of this bone has been directly observed in Lower Carboniferous paleoniscoids from Bear Gulch (Montana, USA; Poplin & Lund 1995).

The absence of the premaxillary results either in the anterior development of the maxillaries which then meet each other above the mouth (e.g. *Aeduella*, Fig. 2C), or in the snout skeleton having a median notch above the mandibular symphysis. Such a notch is observed in Lower Carboniferous rhadinichthyids (Fig. 2A, B) like those from Montana (Poplin & Lund 1995) and Scotland (Moy-Thomas & Dyne 1938). We suspect the presence of this notch in many other paleoniscoid forms which lack the characteristic features of the premaxillary and show, in side view, a typically protruding snout above the aperture of the mouth: for instance *Palaeoniscus* (Fig 2D; Aldinger 1937), *Cycloptychius*, *Elonichthys* (Moy-Thomas & Dyne 1938), *Boreosomus* (Nielsen 1942; Lehman 1952), *Dicellopyge* (Brough 1931).

Schaeffer's description suggests that the Redfieldiidae (Fig. 2E) probably also had this anterior notch (1967: 307, 308): "As the mandibles are about the same length as the infraorbital ramus of the maxilla, the toothlike denticles along rhe ventral margin of the rostral and the antorbital could not have functioned in seizing prey. Furthermore, it has not been possible to reconstruct [...] the snout [...] in a way that would permit the rostral teeth to meet the mandibular ones, even if the lower jaws were actually longer. Part of the space between antorbitals must have been occupied by the mandible when the mouth was completely closed, but we have been unable to eliminate the resulting space between the ventral margin of the rostral and the mandibular symphysis." The presence of an anterior notch is confirmed, according to us, by the characteristic protruding snout in side view, as explained above.

In this peculiar redfieldiid snout, covered with a quantity of small dermal tubercles, what could be the function of an anterior notch? First it could cause a smaller aperture of the mouth and, thus, increase the inhaling strength during expansion of the mouth: this would facilitate

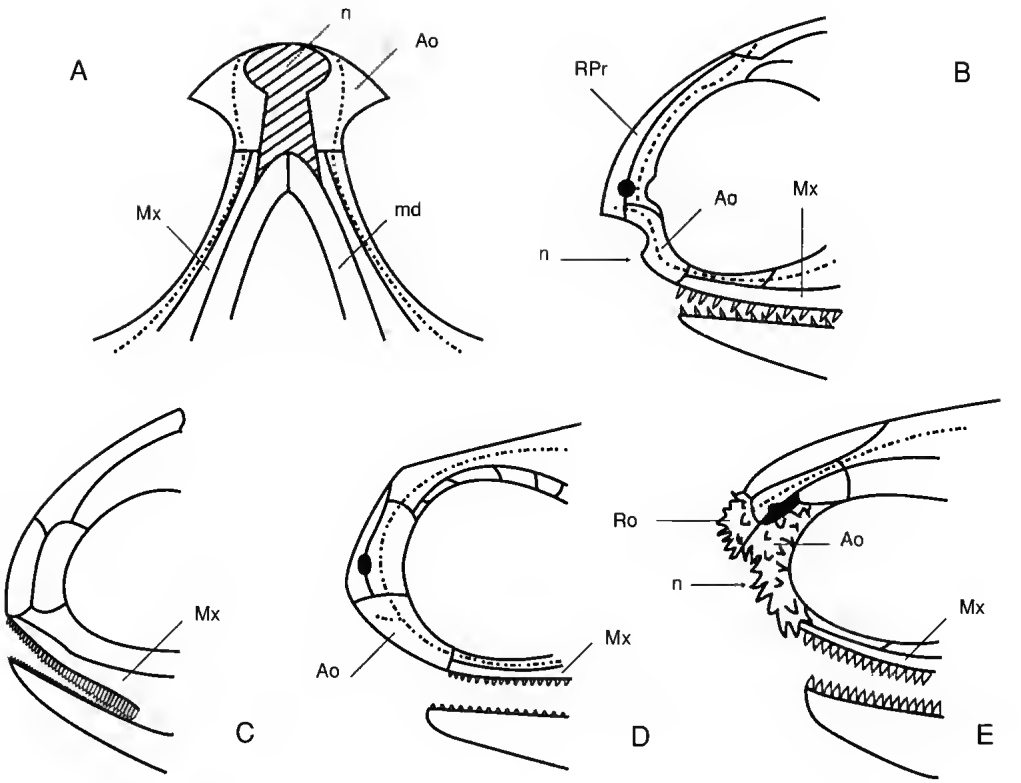

FIG. 2. — Dermal snouts: **A**, ventral view; **B-E**, left lateral view. **A**, **B**, Rhadinichthyid from Bear Gulch (after Lund & Poplin in prep.); **C**, *Aeduella* (after Heyler 1969, fig. 92); **D**, *Palaeoniscus freieslebeni* (after Aldinger 1937, fig. 25B); **E**, *Cionichthys greeni* (after Schaeffer 1967, fig. 7). **Ao**, antorbital; **Mx**, maxillary; **md**, mandible; **n**, notch; **Ro**, rostral; **RPr**, rostro-postrostral.

suction in a benthic feeding mode (Lund *et al.* 1985). Indeed, this combination of an armored projecting snout and the notch would permit these fishes to root around (like hogs), using the denticles to stir up the sediment and the notch to facilitate suction upon those prey items that were scared out of their hiding places. Moreover, Schaeffer and Hutchinson emphasize that these fishes could have had a thick fleshy lip supported by these denticles and overhanging the mouth: this lip helped them to feed at the sediment-water interface, somewhat like the protrusive mouth of recent teleosts. In this hypothesis could an anterior notch have been linked to a very short appendage like a tiny trunk? Like the protrusive premaxillae in recent teleosteans, this would increase the buccal volume during abduction of the lower jaw, as well as just after the food was engulfed and the mouth was closed again (Alexander 1967).

The existence of this anterior notch raises the question of the anatomy of the underlying endocranial and visceral regions: ethmoidal endoskeleton and vomers, as well as oral valves, if there were any in these fishes. In the total absence of data it is difficult to answer.

DISCUSSION ABOUT THE PRIMITIVE STATE AND FURTHER EVOLUTIONARY TRENDS OF THE ACTINOPTERYGIAN PREMAXILLARY

The anatomical variety of the premaxillary in primitive fossil actinopterygians, briefly described above, leads to two fundamental questions:
– What was the condition of the premaxillary, in the ancestral morphotype of actinopterygians?
– What does this variety indicate about the relationships of the main actinopterygian lineages?

In the past the three following hypotheses (absent, fused to other bones, present) have been proposed concerning the ancestral condition of the premaxillary in actinopterygians.

HYPOTHESIS 1

Absence of the premaxillary: Westoll (1937) was among the first to speculate about the fate of the premaxillary. He noticed that the holostean and teleostean premaxillary was quite complex and different from what was known of paleoniscoids at his time. Therefore he thought that the very first actinopterygians had no premaxillary and he proposed four schemes to explain the existence of a premaxillary in the upper actinopterygians: (1) it is a neoformation; (2) it results from a fragmentation of the paleoniscoid rostral; (3) the primitive maxillary has been split into maxillary and premaxillary; (4) or the lineages which gave rise to the upper actinopterygians have been separated very early from the paleoniscoid ones, which implies that premaxillaries developed independantly in both groups. Westoll considered this last hypothesis as improbable. The first of Westoll's suggestions can now be discarded since all other osteichthyan groups share the plesiomorphous occurrence of a premaxillary. Westoll's other schemes are early previews of the subsequent hypotheses stated below (premaxillary produced by fragmentation of compound bones, very early separation of the lineages leading to paleoniscoids and neopterygians, parallelism of eventual structures).

HYPOTHESIS 2

Presence of the premaxillary as a compound bone, macromeric snout: many authors, such as Pehrson (1947, 1958), Gardiner (1963, 1984) and Jessen (1968) suggested that a premaxillary was present in the first actinopterygians but as a rostro-premaxillo-antorbital. This view, based on the observation that this compound bone is present in the most primitive Devonian forms and in the Recent *Polypterus*, is part of the more generalized hypothesis of a macromeric primitive pattern of the dermal snout (Gardiner 1963; Patterson 1975). Later in actinopterygian history, different and successive splittings of the rostro-premaxillo-antorbital would have led to the various dispositions observed in paleoniscoids and to the mesomeric snout anatomy of neopterygians (Fig. 3).

HYPOTHESIS 3

Presence of an individualized premaxillary: mesomeric snout evolving by fragmentations. The ancestral actinopterygian morphotype *has* indeed independant premaxillaries in a mesomeric snout (Pearson 1982; Schaeffer 1984; Long 1988; Gardiner & Schaeffer 1989). This is more consistent with the mesomeric snout disposition of sarcopterygians and of the larval *Polypterus* than with Westoll's first three schemes or with that of a macromeric primitive pattern. We note that this hypothesis fits better with the more recent data about the pattern of occurrence of separate premaxillaries among the paleoniscoids.

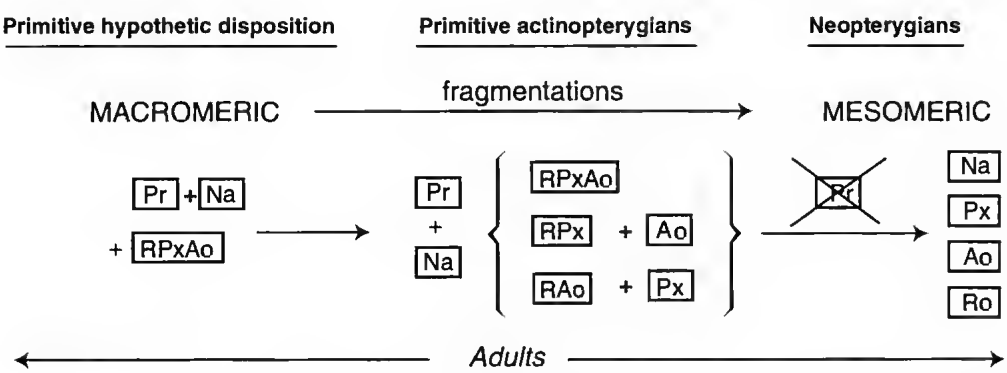

FIG. 3. — Hypothesis about the evolution of the dermal snout after Pehrson (1947, 1958), Gardiner (1963, 1984), Jessen (1968), and others (see text). **Ao**, antorbital; **APx**, antorbito-premaxillary; **Na**, nasal; **Px**, premaxillary; **Pr**, postrostral; **RAo**, rostro-antorbital; **Ro**, rostral; **RPx**, rostro-premaxillary; **RPxAo**, rostro-premaxillo-antorbital; **RPr**, rostro-postrostral.

The lack of premaxillary is better explained as a mere lack of its territory in the embryo rather than as an involution during later development (Poplin & Lund 1995). In order to specify this third hypothesis, Schaeffer (1984: 5) adds that "[...] the pattern in the 24 mm *Polypterus* represents the primitive actinopterygian larval condition, whereas that in the mature *Polypterus* [...] may be regarded as the primitive adult condition."

Therefore, based on this view, the third hypothesis is completed as follows when we add the recent data (Fig. 4). The primitive larval pattern of the snout in actinopterygians was mesomeric with separate postrostrals, rostrals, nasals, premaxillaries and antorbitals. Different processes during development and maturation led to the various dispositions observed in the primitive fossil adult actinopterygians: (1) fusions leading to the variety of macromeric snouts observed in primitive fossil actinopterygians; (2) precocious disappearances during development of its territory resulting in the absence of premaxillary; and (3) neoteny maintaining the larval pattern in adults (Jollie 1969). The neopterygian adult pattern (also characterized by the absence or fusion of a postrostral) sprung after paedomorphosis either from already known lineages of mesomeric primitive actinopterygians, or directly from the primitive hypothetic larval pattern.

CONCLUSION

We propose the following hypothesis about the mechanisms which gave rise to the main patterns of the dermal snout in actinopterygians: the primitive mesomeric snout evolved and diversified either through heterochronous processes, such as neoteny and paedomorphosis, either through fusions or disappearances. This hypothesis leads to the following considerations.

– The ancestral larval morphotype of the acti-

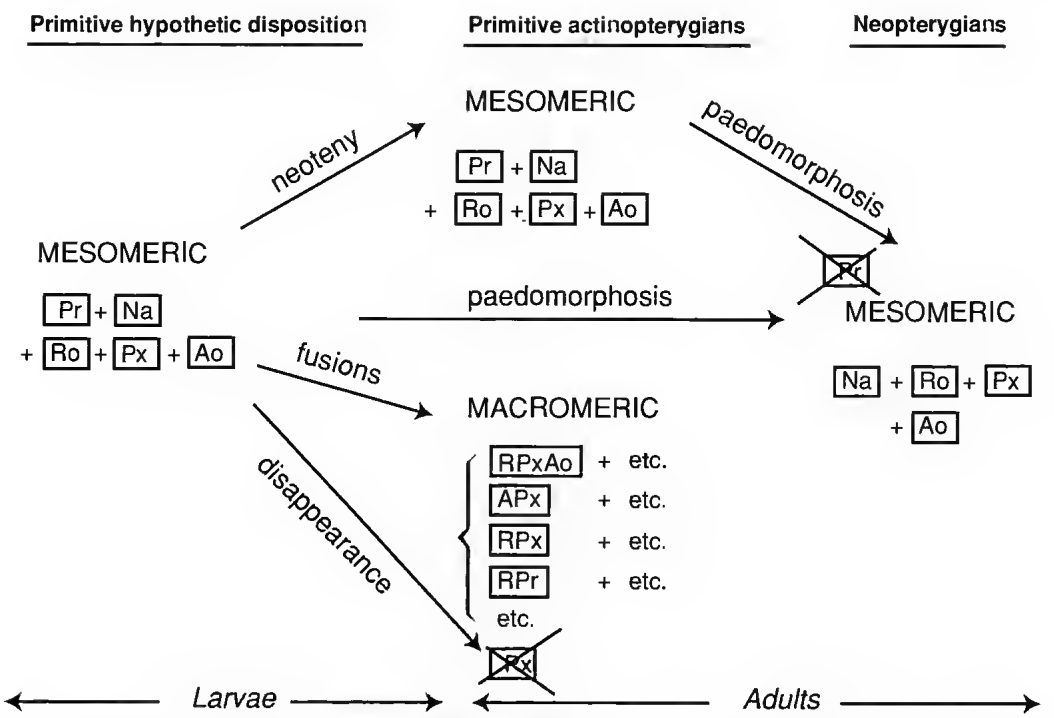

FIG. 4. — Hypothesis proposed in this paper about the evolution of the dermal snout, based on those of Pearson, Schaeffer, Long, Gardiner & Schaeffer (see text). **Ao**, antorbital; **APx**, antorbito-premaxillary; **Na**, nasal; **Px**, premaxillary; **Pr**, postrostral; **Ro**, rostral; **RPx**, rostro-premaxillary; **RPxAo**, rostro-premaxillo-antorbital; **RPr**, rostro-postrostral.

nopterygians is likely to have been provided with a separate premaxillary.
– It is more parsimonious, from a phylogenetic point of view, to think that the lineages with a mesomeric disposition and possessing a premaxillary are more closely related to neopterygians than the other lineages (macromeric and/or lacking premaxillaries).
– The multiple states of the premaxillary (particularly its loss) and their systematic distribution indicate that, at least some of them could have appeared more than once. These data and new informations on the actinopterygian relationships of *Polypterus* can be interpreted as supporting the hypothesis that the lower actinopterygians conveniently called "paleoniscoids" may not be a natural group.

Finally, this review of the problems concerning the primitive pattern of the premaxillary, and of its subsequent evolutionary trends, is a demonstration of the parallel evolution of knowledge and ideas. It is rather amusing to notice that Westoll's first three schemes are invalidated by recent data, and that his last scheme, that he considered as the less likely, turned to be the one favoured herein. In sixty years from now, what will remain of the analysis exposed in this paper?

Acknowledgments
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Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France)

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ABSTRACT
Numerous isolated cynodont teeth have been collected from the Late Triassic of Saint-Nicolas-de-Port (north-eastern France). The material is very diversified and the following taxa are recognized: *Pseudotriconodon wildi* Hahn, Lepage *et* Wouters, 1984; *Tricuspes tuebingensis* E. v. Huene, 1933; *Tricuspes sigogneauae* Hahn, Hahn *et* Godefroit, 1994; *Tricuspes tapeinodon* n.sp.; *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994; *Hahnia obliqua* n.g., n.sp.; *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987; *Lepagia gaumensis*, Hahn, Wild *et* Wouters, 1987; *Maubeugia lotharingica* n.g., n.sp.; *Rosieria delsatei* n.g., n.sp. and aff. *Microscalenodon*. This cynodont fauna mainly includes small insectivorous forms, more particularly represented by Dromatheriidae; tiny herbivorous are represented by rare dwarf Traversodontidae. The study of the palaeogeographical and stratigraphic distribution of the Late Triassic to Early Jurassic cynodonts indicates that the fauna discovered in Saint-Nicolas-de-Port is characteristic of the Late Norian-Rhaetian period and is actually the most representative of this period for Western Europe. Granulometric analysis of the bone-bed reveals that they accumulated in a nearshore shallow marine environment.

KEY WORDS
Cynodontia,
Late Triassic,
Saint-Nicolas-de-Port,
dental morphology.

RÉSUMÉ

De nombreuses dents isolées de cynodontes ont été découvertes dans le Trias supérieur de Saint-Nicolas-de-Port (nord-est de la France). Le matériel étudié est très diversifié et les taxa suivants sont représentés : *Pseudotriconodon wildi* Hahn, Lepage *et* Wouters, 1984 ; *Tricuspes tuebingensis* E. v. Huene, 1933 ; *Tricuspes sigogneauae* Hahn, Hahn *et* Godefroit, 1994 ; *Tricuspes tapeinodon* n.sp. ; *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994 ; *Hahnia obliqua* n.g., n.sp. ; *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987 ; *Lepagia gaumensis*, Hahn, Wild *et* Wouters, 1987 ; *Maubeugia lotharingica* n.g., n.sp. ; *Rosieria delsatei* n.g., n.sp. et aff. *Microscalenodon*. La faune de cynodontes est surtout composée de petits insectivores, représentés notamment par les Dromatheriidae ; de minuscules herbivores, formes naines de la famille des Traversodontidae, sont également présents. L'étude de la répartition paléogéographique et stratigraphique des cynodontes du Trias supérieur et du Jurassique inférieur montre que la faune de Saint-Nicolas-de-Port est caractéristique de la période Norien supérieur-Rhétien ; c'est incontestablement la faune la plus représentative de cette période pour l'Europe de l'Ouest. L'analyse granulométrique du sédiment du *bone-bed* a révélé qu'il s'était accumulé dans un environnement marin proche du rivage.

MOTS CLÉS
Cynodontia,
Trias supérieur,
Saint-Nicolas-de-Port,
morphologie dentaire.

INTRODUCTION

In 1851, Levallois recorded fossil bones from the "*grès infra-liasique*" in the vicinity of Saint-Nicolas-de-Port (Meurthe-et-Moselle, north-eastern France; Fig. 1). In 1862, he mentioned the presence of a layer rich in fish and saurian remains to the south of this town. In 1928, Corroy mentioned Saint-Nicolas-de-Port among the most important upper Keuper localities of Lorraine.

In 1971, Laugier gave the stratigraphic log in a sand quarry opened in 1922, 2.5 km south-east of Saint-Nicolas-de-Port. This quarry falls partly within the boundary of the adjacent village Rosières-aux-Salines. He also documented the diversity and abundance of the fauna discovered there. The stratigraphy and the sedimentology of this section was studied in detail by Al Khatib (1976).

The first mammal-like tooth was discovered in 1975 by G. Wouters, a Belgian collector. This tooth was subsequently described by Russell *et al.* (1976). Since then, several tons of sediments have been washed and screened by G. Wouters, teams from the Muséum national d'Histoire naturelle (Paris) and from the Institut royal des Sciences naturelles de Belgique and several amateur collectors. Attention was particularly paid to mammal teeth discovered in this quarry: these have been described in a series of papers by a team lead by D. Sigogneau-Russell (Sigogneau-Russell 1978, 1983a, 1983b, 1983c, 1989, 1990; Frank *et al.* 1984, 1986; Sigogneau-Russell *et al.* 1986; Hahn *et al.* 1989, 1991). Amphibian and reptile material has been described by Buffetaut & Wouters (1986), Cuny & Ramboer (1991) and Cuny (1993). Fish remains have been studied by Sigogneau-Russell *et al.* (1979), Martin *et al.* (1981) and Duffin (1993). Synthetic faunal lists are given by Cuny (1993) and Duffin (1993).

Until now, little work has been completed about the cynodont teeth discovered in Saint-Nicolas-de-Port, in spite of their abundance and their scientific interest. The double-rooted mammal-like tooth described by Russell *et al.* (1976) was subsequently named *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994 and referred to the family "Therioherpetidae" (Sigogneau-Russell & Hahn 1994). Hahn *et al.* (1994) described teeth of *Tricuspes sigogneauae* Hahn, Hahn *et* Godefroit, 1994 and reviewed the systematic position of the family Droma-

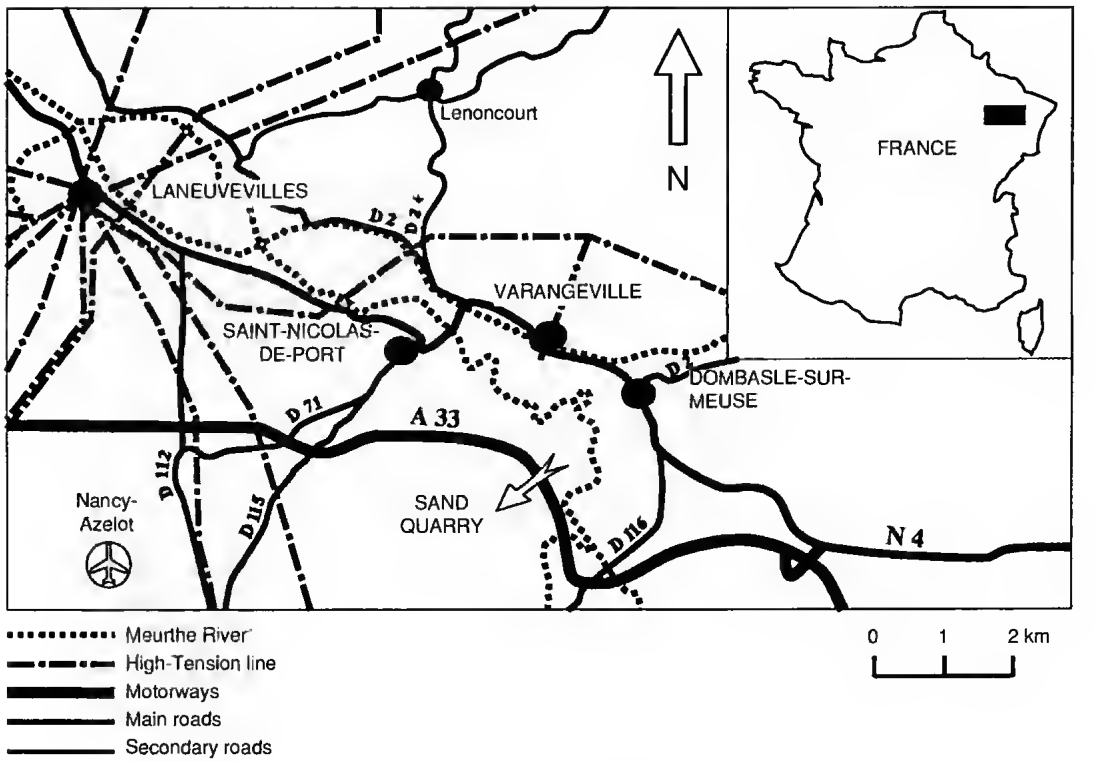

FIG. 1. — Locality sketch map for Saint-Nicolas-de-Port.

theriidae. The purpose of the present paper is to describe the cynodont remains discovered in Saint-Nicolas-de-Port, on the basis of the whole currently available material. The collections are housed in the Institut royal des Sciences naturelles de Belgique (Brussels: IRSNB) and in the Muséum national d'Histoire naturelle (Paris: MNHP). The fossils were collected by G. Wouters, D. Sigogneau-Russell, J.-C. Lepage, D. Delsate and P. Godefroit.

GEOLOGICAL SETTING

Laugier (1971, fig. 19) described the geological section exposed in the quarry of Saint-Nicolas-de-Port. The base of the section is formed by schistose marls of the Keuper. It is overlain by four sedimentary cycles. Bone-beds can be observed at the base of each cycle, followed by sands and sandstones, finally by clays. The bone-beds decrease in thickness through the sequence. The basal conglomerate, above the Keuper marls, reaches a thickness of 1.05 m.

Unfortunately, the quarry is now being used as a city dump and the section described by Laugier cannot be observed any longer. Recent excavations and new sections demonstrate that the geological structure of the quarry is much more complex than described by Laugier. Most of the deposits are lenticular and show, therefore, important lateral variations. Furthermore, correlations between close sections are very difficult to establish.

Most of the vertebrate material discovered since 1975 at Saint-Nicolas-de-Port has been found in only one bone-bed. Figure 2 illustrates the geological section observed in this part of the quarry. The bone-bed is an intra-formational conglomerate which varies in thickness from 0.2 to 1 m. It is formed by coarse sands and small pebbles. It lays upon more than 7 m of alternating marly clays and sands. The bone-bed is capped by nearly 3 m of compact sandstones. Recent excavations exploited other bone-beds in other parts of

the quarry. The sampled sediments have still to be screened and sorted. It is interesting to notice that, nowadays, Keuper marls cannot be observed in any of the recent sections of the quarry. The age of the Saint-Nicolas-de-Port quarry has been much disputed. Lack of international agree-

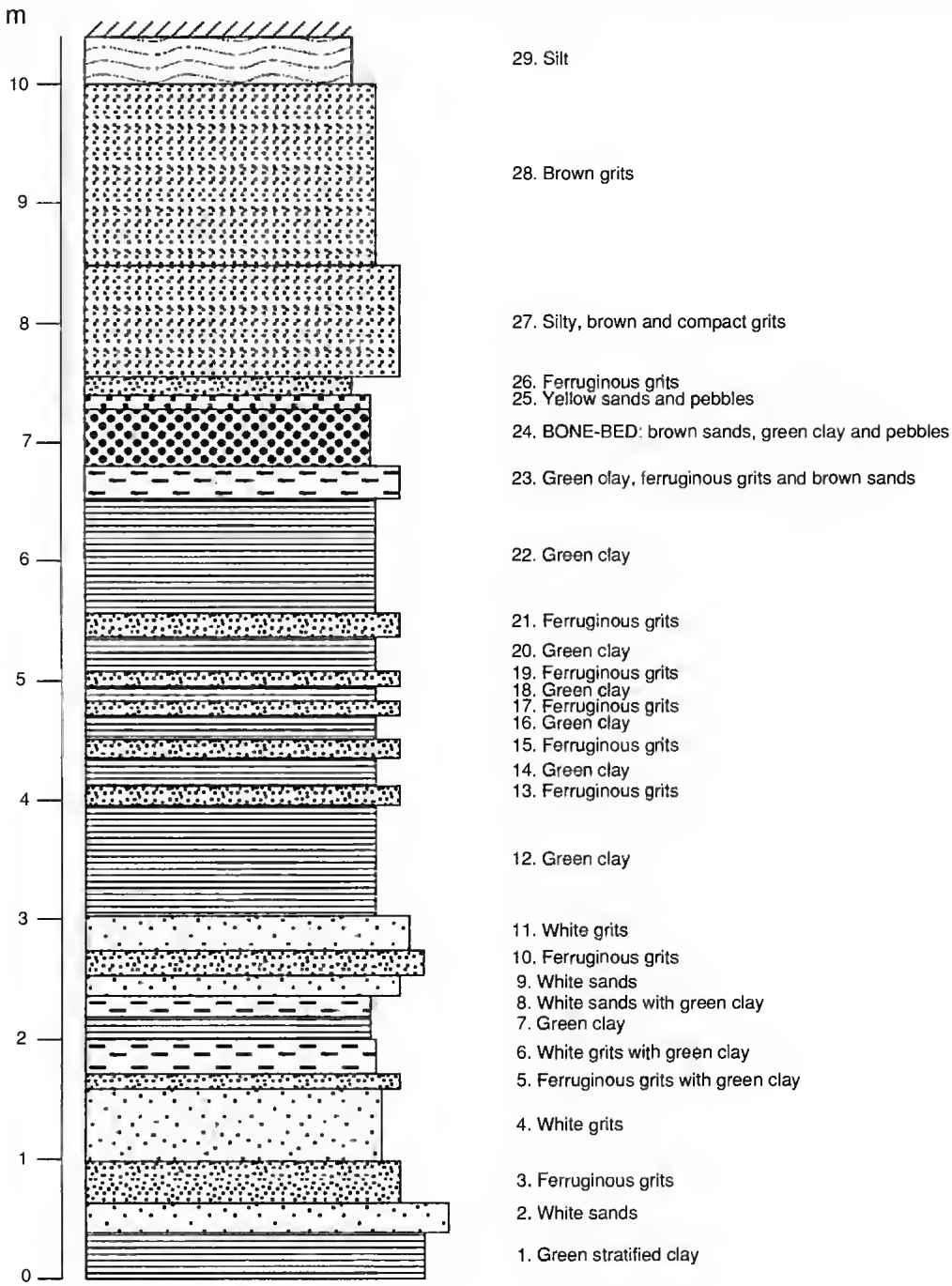

FIG. 2. — Stratigraphic log of the Upper Triassic section at Saint-Nicolas-de-Port.

ment on the status of the Rhaetian Stage limits the discussion. Moreover, palynological samplings in the quarry are, at the present time, unprofitable. From a lithological point of view, the sediments are regarded as Lower Rhaetian in age (Laugier 1971; Al Khatib 1976; Sigogneau-Russell 1983a). Buffetaut (1985), Buffetaut & Wouters (1986), Cuny & Ramboer (1991), Duffin (1993) and Cuny (1993) argue for a slightly older age: the vertebrate fauna from Saint-Nicolas-de-Port shows close similarities to that of the Knollenmergel at Halberstadt in central Germany (Upper Norian).

Granulometric analysis of the sediments (Al Khatib 1976) reveals that they accumulated in a nearshore shallow marine environment. The sands have some characters of river or beach deposits.

SYSTEMATIC PALAEONTOLOGY

The systematics of the Cynodontia adopted by Battail (1991) is followed in the present paper. Concerning the family Dromatheriidae, the classification proposed by Hahn *et al.* (1994) is followed. As the taxa treated in the present paper are defined exclusively on dental characters, it is usually difficult to settle with certainty the polarity of these traits. For that reason, it has been decided to include both apomorphic and plesiomorphic characters in the diagnoses of Cynodontia *incertae sedis* taxa; therefore, these do not follow strictly the cladistic principles.

Order THERAPSIDA Broom, 1905
Infraorder CYNODONTIA Owen, 1861

CYNODONTS WITH SECTORIAL POST-CANINE TEETH

ORIENTATION OF THE TEETH

The orientation of isolated teeth in cynodonts with sectorial teeth is discussed by Peyer (1956), Russell *et al.* (1976) and Hahn *et al.* (1984, 1987, 1994). The most convex side is conventionally and somewhat arbitrarily regarded as the labial side, on both the upper and lower post-canines. The distal inclination of the cusps, when present, determines the mesial and distal sides of the teeth. The accessory cusps are usually more numerous or better developed on the distal half of the crown than on the mesial half. When wear is developed, it is possible to distinguish the upper teeth from the lower ones: wear develops on the lingual side of the former and on the labial side of the latters. When wear is not developed or when the lingual and labial sides of the crown are symmetrical, it is thus impossible to settle wherher the specimen belongs to the upper or to the lower tooth row.

Family DROMATHERIIDAE Gill, 1872

REMARK

The cladogram of the Dromatheriidae proposed by Hahn *et al.* (1994) shows that this group is clearly paraphyletic, as the ancestry of the mammals lies within it.

Genus *Pseudotriconodon*
Hahn, Lepage *et* Wouters, 1984

Pseudotriconodon Hahn, Lepage *et* Wouters, 1984: 358.

TYPE SPECIES. — *Pseudotriconodon wildi* Hahn, Lepage *et* Wouters, 1984.

OTHER REFERRED SPECIES. — *Pseudotriconodon chatterjeei* Lucas *et* Oakes, 1988. Identification of this taxon as a cynodont has been questioned by Sues & Olsen (1990), but without argumentation.

DIAGNOSIS. — Crown of postcanine teeth tricuspid to pentacuspid and very narrow (2.4 < ratio "length/width" of the crown < 4.2); labial and lingual sides of the crown nearly parallel. Cutting edge perfectly straight. Base of the crown not constricted. Root semielliptical in outline, about 1.5 times as high as the crown; tip of the root sometimes divided by a short furrow; pulpal canal small, elliptical in shape and sometimes double.

Pseudotriconodon wildi
Hahn, Lepage *et* Wouters, 1984
(Figs 3, 4)

Pseudotriconodon wildi Hahn, Lepage *et* Wouters, 1984: 358, pl. 1, figs 1, 2; pl. 2, figs 2-6; pl. 3, figs 1-6. – Clemens 1986: 238. – Hahn *et al.* 1987: 17,

pl. 5, fig. 2. – Lucas & Oakes 1988: 447. – Battail 1991: 88. – Hahn *et al.* 1994: 142, fig. 2a. – Sigogneau-Russell & Hahn 1994: 206, fig. 10.10d.

HOLOTYPE. — MNHL "R.M. 1", in the Muséum national d'Histoire naturelle de Luxembourg.

LOCUS TYPICUS. — "Rinckebierg" (Medernach, Great-Duchy of Luxembourg).

STRATUM TYPICUM. — Bone-bed included within the Steinmergel-Gruppe (Norian, Upper Triassic).

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: IRSNB R156, IRSNB R157, IRSNB 28114/68, IRSNB 28114/100, IRSNB 28114/638, IRSNB 28114/737, IRSNB 28114/739, IRSNB 28114/752, IRSNB 28114/811, IRSNB 28114/859, IRSNB 28114/870, IRSNB 28114/905, IRSNB 28114/906, IRSNB 28114/994, MNHP SNP25, MNHP SNP54, MNHP SNP115L, MNHP SNP61W, MNHP SNP63, MNHP SNP68W, MNHP SNP75W, ? MNHP SNP83W, MNHP SNP198W, MNHP SNP288W, MNHP SNP295W, MNHP SNP300W, MNHP SNP306W, ?MNHP SNP337W, MNHP SNP351W, MNHP SNP423W, MNHP SNP425W.

DIAGNOSIS. — 0.9 mm < length of the crown of postcanine teeth < 3.1 mm; 0.35 mm < width of the crown of postcanine teeth < 0.95 mm.

DESCRIPTION

Classification

Hahn *et al.* (1984) base their classification of the postcanine teeth in *Pseudotriconodon wildi* on the number and the arrangement of the accessory cusps. Six categories can be distinguished.

Group I:
1 anterior and 1 posterior accessory cusps.
Group II:
1 anterior and 2 posterior accessory cusps.
Group III:
1 anterior and 3 posterior accessory cusps.
Group IV:
2 anterior and 2 posterior accessory cusps.
Group V:
2 anterior and 3 posterior accessory cusps.
Group VI:
? anterior and 2 posterior accessory cusps.

Measurements

The measurements taken on the postcanine teeth of *Pseudotriconodon wildi* are shown in table 1. The orientation of the teeth and the measurements are illustrated by Hahn *et al.* (1984, fig. 1).

Crown

In occlusal view, the crown appears elongated antero-posteriorly and quite narrow labio-lingually: in the specimens discovered in Saint-Nicolas-de-Port, the ratio "length/width" of the crown varies between 2.45 and 4.45. Both the lingual and the labial sides of the crown are

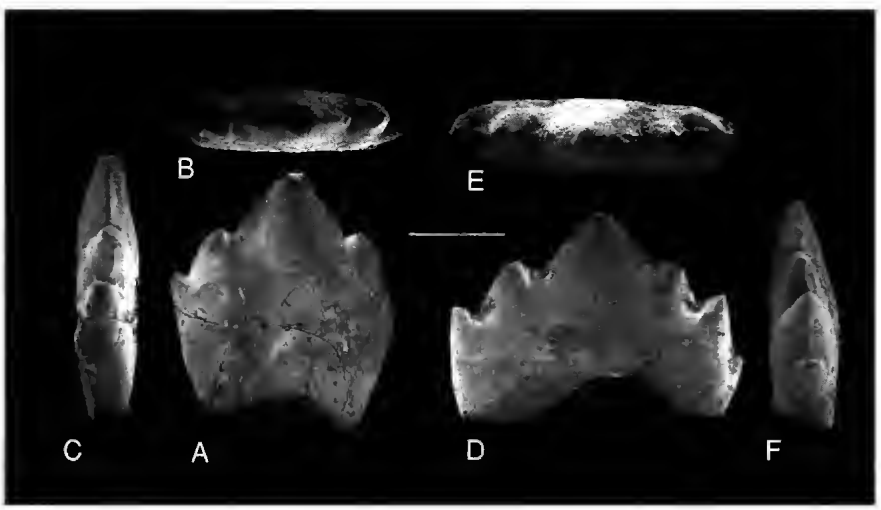

FIG. 3. — Postcanine teeth of *Pseudotriconodon wildi*, from the Late Triassic of Saint-Nicolas-de-Port. **A-C**, IRSNB R156; **A**, lateral view; **B**, occlusal view; **C**, posterior view. **D-F**, IRSNB R157; **D**, lateral view; **E**, occlusal view; **F**, posterior view. Scale bar: 1 mm.

nearly straight, slightly convex at the level of the main central cusp. All the cusps are in line with the antero-posterior axis of the crown. The cutting edge is very sharp and perfectly straight.

In anterior and posterior views, all the cusps are nearly perfectly straight, without marked curve towards the lingual side of the crown.

In lateral view, the main cusp occupies a median position. It has the outline of an isosceles triangle; its anterior and posterior edges are straight or slightly convex. It is flanked by one to two anterior and one to three posterior accessory cusps of decreasing heights. All are triangular, sharp and clearly separated from each other. Their vertical axes usually diverge slightly from the main cusp; they can be curved towards the

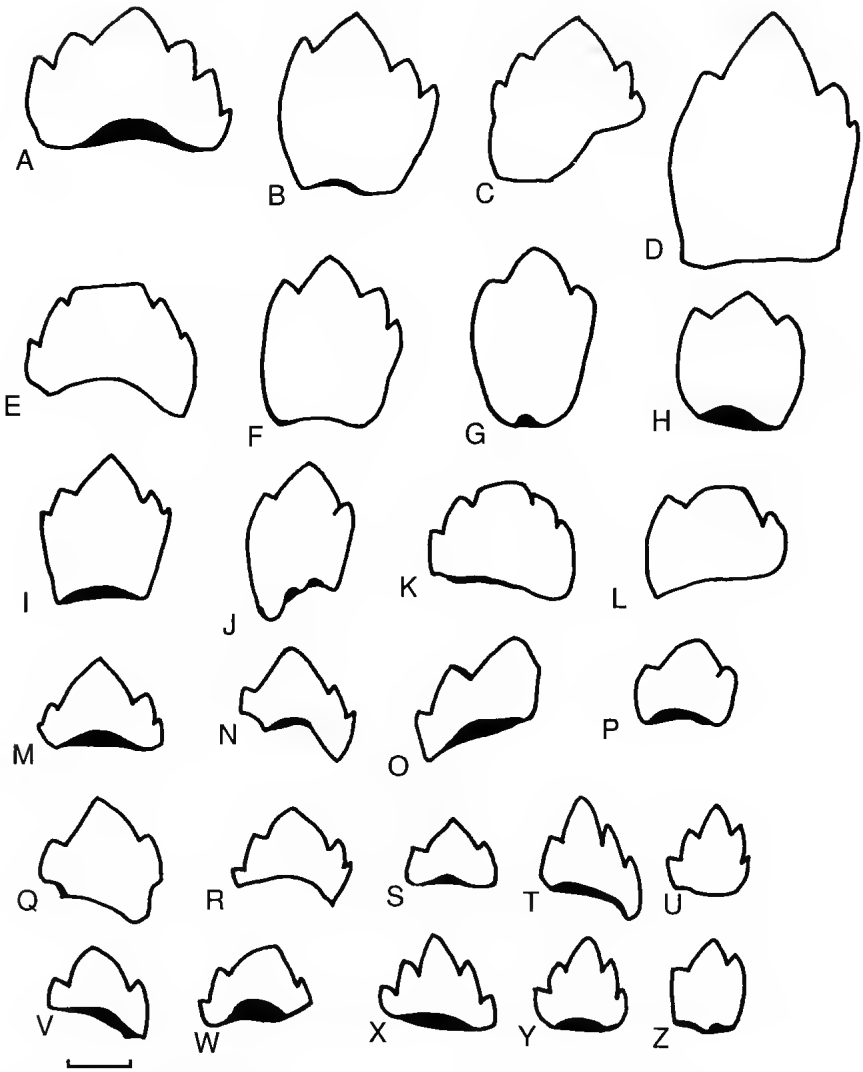

FIG. 4. — Outline of postcanine teeth of *Pseudotriconodon wildi*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, IRSNB R157; **B**, IRSNB R156; **C**, IRSNB 28114/859; **D**, IRSNB 28114/739; **E**, IRSNB 28114/906; **F**, MNHP SNP300W; **G**, IRSNB 28114/737; **H**, MNHP SNP306W; **I**, MNHP SNP63W; **J**, IRSNB 28114/68; **K**, IRSNB 28114/905; **L**, IRSNB 28114/752; **M**, IRSNB 28114/870; **N**, IRSNB 28114/627; **O**, IRSNB 28114/766; **P**, IRSNB 28114/100; **Q**, MHNP SNP115L; **R**, MNHP SNP425W; **S**, MHNP SNP68W; **T**, MNHP SNP75W; **U**, MNHP SNP351W; **V**, IRSNB 28114/811; **W**, IRSNB 28114/994; **X**, MNHP SNP423W; **Y**, MNHP SNP295W; **Z**, MNHP SNP288W. Scale bar: 1 mm.

median axis of the crown.
The wear on the cusps is apical but very erratic: it does not form clearly defined facets. It is therefore usually impossible to distinguish upper and lower postcanines. The crown has no basal cingulum and no basal groove separating the crown from the root.

Root
The root is about 1.5 times as high as the crown. Its outline is semielliptical in lateral view. Its median portion is slightly depressed in comparison with the anterior and the posterior borders. The pulpal foramen, when it can be observed, is elliptical and elongated antero-posteriorly. Neither bipartition of the root nor undoubling of the pulpal canal can be observed in the teeth discovered in Saint-Nicolas-de-Port. In anterior view, the root is very compressed labio-lingually, like the crown.

TABLE 1. — Measurements (in mm) of the postcanine teeth of *Pseudotriconodon wildi*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown. For the signification of the groups, see text.

Group	Number	Lc	Wc	Hc	L/W
I	IRSNB 28114/737	1.95	0.55	1.1	3.55
	IRSNB 28114/68	1.65	0.6	1.15	2.75
	IRSNB 28114/628	2.1	0.55	1.4	3.82
	IRSNB 28114/752	2	0.5	>1.65	4
	IRSNB 28114/811l	1.7	0.7	1.3	2.43
	RSNB 28114/100	1.65	0.55	1	3
	MNHP SNP54	1.5	0.37	1.1	4.05
	MNHP SNP 115L	1.65	0.5	1.15	3.3
	MNHP SNP61W	2.37	0.9	-	2.63
	MNHNP SNP68W	1.35	0.55	-	2.45
	MNHNP SNP288W	1.1	0.25	0.9	4.4
	MNHP SNP306W	1.9	0.45	1.15	4.22
II?	IRSNB 28114/994	?1.8	0.65	1.3	?2.77
II	IRSNB R156	2.45	0.75	1.85	3.27
	IRSNB 28114/739	2.85	0.95	2.25	3
	MNHP SNP75W	1.42	0.55	-	2.58
	MNHP SNP300W	2.18	0.55	1.45	3.96
IV	IRSNB 28114/859	2.25	0.7	1.5	3.21
	IRSNB 28114/905	2.25	0.6	>1.6	3.75
	IRSNB 28114/870	?2	0.7	1.45	?2.86
	IRSNB 28114/906	2.55	0.85	>2	3
	MNHP SNP63W	2	0.45	1.4	4.44
	MNHP SNP295W	1.35	0.45	1.05	3
	MNHP SNP351W	1.15	0.4	1.1	2.88
	MNHP SNP423W	1.75	0.6	-	2.92
	MNHP SNP425W	1.7	0.55	-	3.09
V	IRSNB R157	3.1	0.75	2.1	4.13

DISCUSSION

Small teeth with fundamentally tricuspid crowns and undivided roots are also known, in Triassic times, in *Tanystropheus*, *Macrocnemus* (Prolacertilia) and *Eudimorphodon* (Pterosauria). Hahn *et al.* (1984) list the features distinguishing the teeth of these animals. Differences can particularly be observed in the structure of the root, but also in the ornamentation of the enamel or in the proportions of the crown. During the Late Triassic, *Pseudotriconodon* and *Eudimorphodon* lived together in Saint-Nicolas-de-Port (Godefroit & Cuny, in prep.), as in Medernach (Great-Duchy of Luxemburg, Hahn *et al.* 1984) and in the Chinle Formation of New Mexico, USA (Murry 1986; Lucas & Oakes 1988).
In contemporary Morganucodontidae (real mammals), the root in premolars and molars is completely divided; moreover, the crown is surrounded by well developed cingula.
Ornithischian dinosaurs from Late Triassic assemblages of North America also possess multicuspid triangular teeth (Hunt & Lucas 1994). In these animals the crowns are more massive and usually recurved (at least in the premaxillary teeth). The cusps are more numerous and much less distinct. The root is higher and separated from the crown by a well developed neck.
The genus *Pseudotriconodon* is now unanimously referred to the Family Dromatheriidae (Carroll 1988; Lucas & Oakes 1988; Battail 1991; Hahn *et al.* 1994; Sigogneau-Russell & Hahn 1994): this attribution is based on the partial bipartition of the root observed in some specimens, on the triconodont organization of the crown and on the combinated absence of cingula and constriction between the crown and the root.
The teeth from Saint-Nicolas-de-Port differ from *Pseudotriconodon chatterjeei*, from the Chinle Formation of New Mexico, by the absence of distinct striations on the enamel and by their larger size. They are both morphologically and morphometrically closer to *Pseudotriconodon wildi*, from Medernach.

Figure 5 shows the relative evolution of the length (x axis, in Ln) and of the width (y axis, in Ln) of the dental crowns in *Pseudotriconodon wildi*. The allometric parameters have been estimated, using

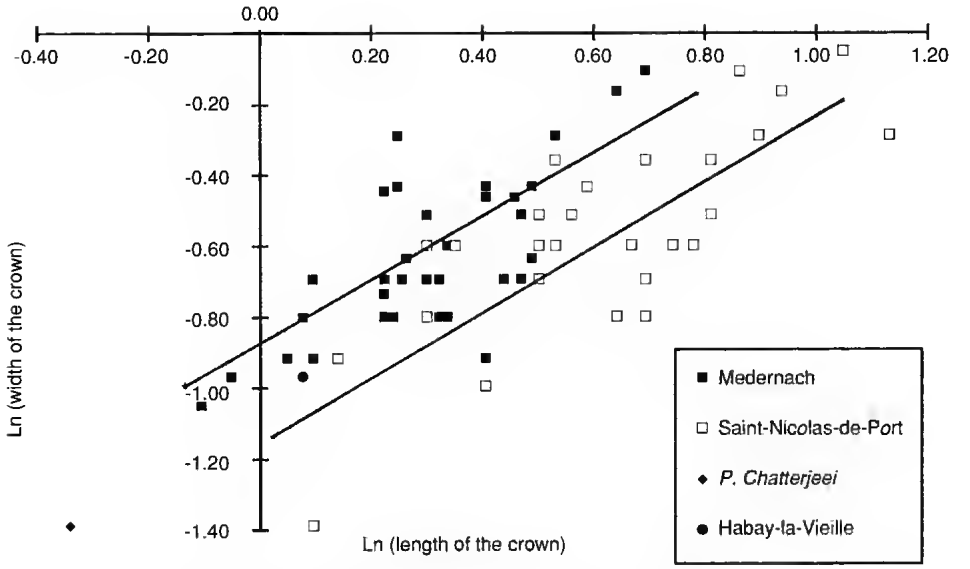

FIG. 5. — Dispersion diagram of the postcanine teeth in *Pseudotriconodon*.

Teissier's (1948) formulas (both the length and the width of the crown are here regarded as dependent variables), separately for the populations from Medernach and Saint-Nicolas-de-Port. The allometry coefficient is similar in both population: b = 0.90 and 0.92, respectively in the populations from Saint-Nicolas-de-Port and Medernach. The isometry between the variables can therefore reasonably be concluded. On the other hand, the characteristic ratio differs in the two populations: a = 0.31 and 0.40, respectively in the populations from Saint-Nicolas-de-Port and Medernach. In average, the teeth discovered in Saint-Nicolas-de-Port seem narrower than those from Medernach. This difference cannot be considered as statistically significant because Pearson's correlation coefficients between the variables are not sufficiently high: r = 0.80 for the teeth from Saint-Nicolas-de-Port and 0.73 for the teeth from Medernach. Nevertheless, this observation is quite interesting because it reflects a more general morphometrical trend: Tessier (1936) and Chevais (1937) have actually compiled examples in which local races of a same species do not differ in "b" value, but can be distinguished in "a" value. The proportions of the studied organ differ in these populations, but the differences are preserved without change during the life of the animal (at least, in mature specimens). Therefore, the study of dental allometry in *Pseudotriconodon wildi* shows that the morphometrical differences observed between the teeth discovered in Saint-Nicolas-de-Port and Medernach can be interpreted as normal variations between two local (geographically and/or stratigraphically) faunas of a same species. There is no morphological or morphometrical evidence now available to support a systematic distinction between these populations.

Genus *Tricuspes* E. von Huene, 1933

Tricuspes E. von Huene, 1933: 82.

TYPE SPECIES. — *Tricuspes tuebingensis* E. von Huene, 1933.

OTHER REFERRED SPECIES. — *Tricuspes sigogneauae* Hahn, Hahn *et* Godefroit, 1994; *Tricuspes tapeinodon* n.sp.

DIAGNOSIS. — Accessory cusps sometimes developed on the anterior (F/e) or on the posterior (D/d) border of the molar crown. Cusps not perfectly aligned but arranged in a V-like manner: the anterior and posterior cusps are set in a slightly more lingual position than the more central cusps and the crown has an arched aspect in occlusal view. Axis of the crown perfectly vertical.

Crown separated from the root by a marked constriction. Root subdivided in its full length, but both portions remain in close contact with one another.

Tricuspes tuebingensis E. von Huene, 1933 (Fig. 6A-C)

Tricuspes tübingensis E. von Huene, 1933: 82, pl. 1, fig. 7a, b. – Kuhn 1965: 85.
Tricuspes tubingensis – Hopson & Kitching 1972: 82. – Clemens *et al.* 1979: 10. – Clemens 1980: 66, pl. 10, figs 1, 2a-c. – Battail 1991: 89. – Hahn *et al.* 1994: 148, fig. 3.
? Schneidezähn S_1 – E. von Huene 1933: 84, pl. 1, fig. 9a-d.

HOLOTYPE. — An isolated right molariform preserved in the Geologisch-Paläonrologischen Institut der Universität Tübingen (Germany) and figured, among others, by Clemens (1980, pl. 10, figs 1, 2a-c).

LOCUS TYPICUS. — Gaisbrunnen, north of Tübingen (Württemberg, Getmany).

STRATUM TYPICUM. — "Rhätbonebed", included in Rhaetian sandstones, Upper Triassic.

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: IRSNB R158 (upper molariform).

DIAGNOSIS. — Molariform teeth with a tiny accessory cusp m in postero-lingual position; crown rather high: ratio "length/height" of the crown = 1.53 in IRSNB R158 and < 1.5 in the holotype. Accessory cusps D/d and E/e, when present, incorporated in the cutting edge of the crown.

DESCRIPTION

Measurements

Length of the crown = 2.75 mm; width of the crown = 1.06 mm; height of the crown = 1.8 mm.

Crown

The nomenclature of the cusps in *Tricuspes* is illustrated by Hahn *et al.* (1994, fig. 5). The enamel is perfectly smooth. In occlusal view, the crown is rather elongated: the ratio "length/width" of the crown = 2.59. The labial side is very convex antero-posteriorly and the lingual side, slightly concave. The crown is formed by five very distinct cusps. Contrary to *Pseudotriconodon*, these are not perfectly aligned, but they are arranged in a V-like manner: cusps B and C are set in a more lingual position than cusp A; in the same way, accessory cusps D and E are set in a slightly more lingual position than cusps C and B. The cutting edge is not as developed as in *Pseudotriconodon*. The base of the crown is clearly constricted.

In lingual view, the crown is not very high (ratio "length/height" of the crown = 1.55) and domi-

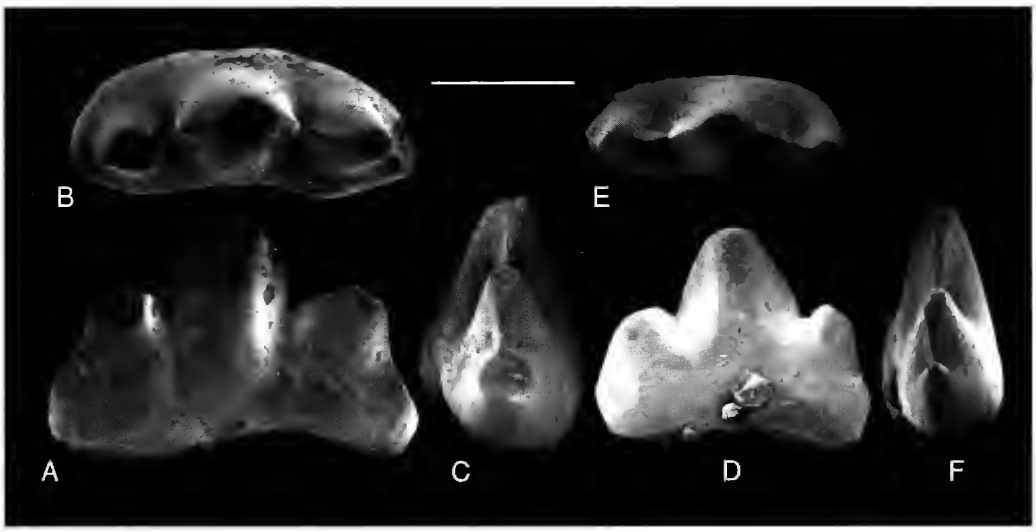

FIG. 6. — **A-C**, IRSNB R158, upper postcanine tooth of *Tricuspes tuebingensis*, from the Late Triassic of Saint-Nicolas-de-Port; lingual view; **B**, occlusal view; **C**, posterior view. **D-F**, IRSNB R159, upper postcanine tooth of *Tricuspes sigogneauae*, from the Late Triassic of Saint-Nicolas-de-Port; **D**, lingual view; **E**, occlusal view; **F**, anterior view. Scale bar: 1 mm.

nated by the median cusp A. The anterior and posterior edges of this cusp are clearly convex and separated from cusps B and C by distinct notches. Its vertical axis slopes slightly backwards. Anterior cusp B is lower than posterior cusp C. The latter slopes more backwards than cusp A; cusp B slopes somewhat forwards. Cusp B is flanked anteriorly by a low, bulbous accessory cusp E; cusp C is posteriorly flanked by a very eroded accessory cusp D. These accessory cusps are incorporated in the cutting edge of the crown. A tiny, very eroded accessory cusp m is visible on the lingual side of the crown, just below cusp C. Wear facets affect the lingual side of the apex of the cusps. This tooth is thus an upper molariform. On cusp A, the wear facet is triangular and very concave. Cusp B is more affected by wear than cusp C. Accessory cusp D, as mentioned above, is very eroded.

Root

The root is not preserved in IRSNB R158.

DISCUSSION

Tricuspes tuebingensis is known by one lower (holotype) and one upper (IRSNB R158) molariform teeth. These teeth differ from those of *Tricuspes sigogneaue* (see below) in the presence of a tiny accessory cusp m on the postero-lingual portion of cusp c. Accessory cusps d and e, although eroded, are also better developed in IRSNB R158 than in *Tricuspes sigogneauae* (see Hahn *et al.* 1994, figs 5-9) and are clearly located on the cutting edge of the crown. IRSNB R158 differs from the holotype by its crown proportionally lower and longer. This character, correlated to the development of accessory cusps d and e, probably reflects a more distal position in the tooth row of the former. Hahn *et al.* (1994) did not observe significant differences in the proportions of lower and upper molariform teeth in *Tricuspes sigogneauae*.

Tricuspes sigogneauae
Hahn, Hahn *et* Godefroit, 1994
(Fig. 6D-F)

Tricuspes sigogneauae Hahn, Hahn *et* Godefroit, 1994: 149, figs 5-13.
Tricuspes cf. *tubingensis* Clemens, 1980: 71, pl. 10, fig. 5a-c.

HOLOTYPE. — MNHP SNP49LW, a lower molariform figured by Hahn *et al.* (1994, fig. 5).

PARATYPES. — 6 upper molars, 7 lower molars and 4 premolars preserved in the MNHP and the IRSNB (see Hahn *et al.* 1994, tabs 2-4, for catalogue numbers).

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

STRATUM TYPICUM. — "Rhaetian" sandstones. Upper Triassic.

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: IRSNB R159, IRSNB 28114/193, MNHNP SNP55, MNHP SNP24W, ? MNHP SNP98W, MNHP SNP289W, MNHP SNP343W, MNHP SNP345W.

DIAGNOSIS. — Molariform teeth without accessory cusp m in postero-lingual position; crown high: ratio "length/height" of the crown < 1.3. Accessory cusps D/d and E/e, when present, not incorporated in the cutting edge of the crown, but located on its anterior and posterior wall.

TABLE 2. — Measurements (in mm) of the new molariform teeth of *Tricuspes sigogneauae*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown; **LL**, lower left; **LR**, lower right; **UL**, upper left; **UR**, upper right.

Number	Position	Lc	Wc	Hc	Lc / Wc	Root	Cusps
IRSNB 28114/193	LL	2.92	1.16	2.8	2.52	+	3
MNHP SNP289W	LR	1.86	0.77	1.75	2.42	-	3 (?)
MNHP SNP24W	UL	2.56	1.1	1.95	2.33	-	+ 3 +
MNHP SNP55	UR	1.67	0.68	1.36	2.46	-	3
IRSNB R159	UR	2.17	0.8	1.75	2.71	-	+ 3 +
MNHP SNP343W	UR	1.13	0.5	1	2.26	-	(?) 3
MNHP SNP345W	UR	-	0.87	2	-	-	+3 (?)

DESCRIPTION

The molariform teeth of this species were very accurately described by Hahn *et al.* (1994). The new material discovered in Saint-Nicolas-de-Port does not give new morphological informations. Table 2 gives a summary of the main morphological and morphometrical informations collected from the new molariforms of *Tricuspes sigogneauae*. The classification of the teeth, following the development of the accessory cusps, was created by Hahn *et al.* (1994) and is explained below (description of *Tricuspes tapeinodon*).

DISCUSSION

Hahn *et al.* (1994, figs 13, 14) attribute four premolariform teeth to *Tricuspes sigogneauae*. These are regarded, in the present paper, as belonging to *Cynodontia* incertae sedis.

Tricuspes tapeinodon n.sp.
(Figs 7, 8)

Tricuspes sp. indet. – Hahn *et al.* 1994: 154, *partim*, fig. 16.

HOLOTYPE. — IRSNB R161, an upper right molariform.

PARATYPES. — IRSNB R160, IRSNB 28114/35, IRSNB 28114/80, IRSNB 28114/106, IRSNB 28114/107, IRSNB 28114/108, IRSNB 28114/109, IRSNB 28114/827, IRSNB 28114/988, MNHP SNP160W.

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

DERIVATIO NOMINIS. — *tapeinos* (Greek) = low, and *odous* (Greek) = tooth.

STRATUM TYPICUM. — "Rhaetian" sandstones. Upper Triassic.

DIAGNOSIS. — Crown of the molariform teeth very low: ratio "length/height" of the crown > 1.55. Median cusp A/a not much higher than cusps B/b and C/c. No accessory cusp m in postero-lingual position. Accessory cusps d and e, when present, incorporated in the cutting edge of the crown.

DESCRIPTION

Classification

As proposed by Hahn *et al.* (1994) in *Tricuspes sigogneauae*. 3; both accessory cusps D/d and E/e absent; + 3: E/e present, D/d absent; 3 +: E/e absent, D/d present; +3+: both D/d and E/e present.

Measurements

The measurements taken on the molariform teeth of *Tricuspes tapeinodon* are shown in table 3.

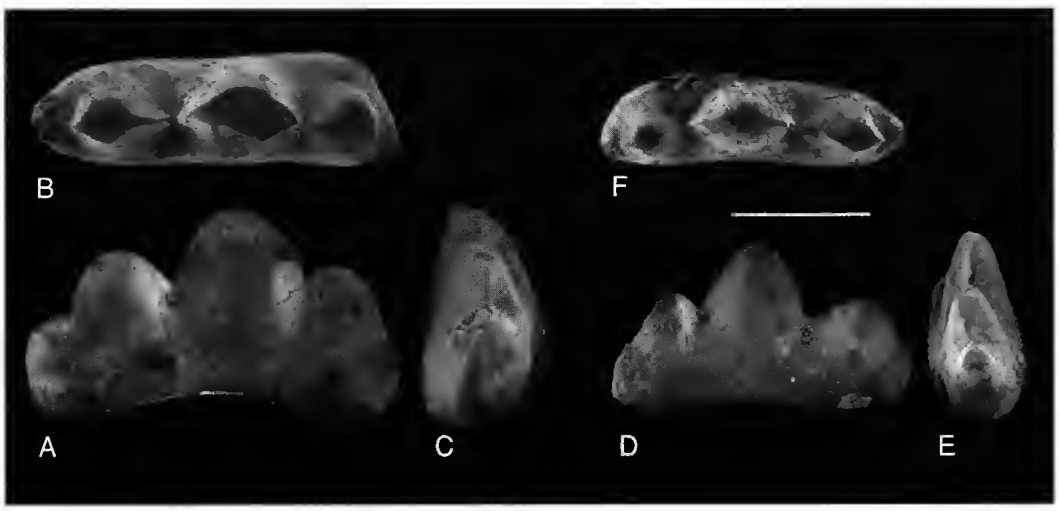

FIG. 7. — Molariform teeth of *Tricuspes tapeinodon*, from the Late Triassic of Saint-Nicolas-de-Port. **A-C**, IRSNB R161, upper postcanine; **A**, lingual view; **B**, occlusal view; **C**, anterior view. **D-F**, IRSNB R160, ? lower postcanine; **D**, lingual view; **E**, posterior view; **F**, occlusal view. Scale bar: 1 mm.

Crown

The enamel is always perfectly smooth. The crown is composed of three main cusps. The highest (A/a) is set in a submedian position and flanked by an anterior cusp (B/b) and a posterior cusp (C/c). Two accessory cusps are sometimes developed on the anterior and posterior portion of the crown (respectively E/e and D/d). In occlusal view, the crown is proportionally long and narrow: the ratio "length/width" of the crown varies between 2.25 and 3.8, on the teeth currently studied. The crown has a pronounced arched aspect: its labial side is very convex antero-posteriorly and its lingual side, slightly concave; at the level of the central cusp, the lingual side of the crown is nevertheless somewhat convex. As usual in *Tricuspes*, the cusps are not perfectly aligned, but set in a V-like manner. The cutting edge joining the cusps together is less developed than in *Tricuspes tuebingensis* or *Tricuspes sigogneauae*. The anterior and posterior ends of the crown are tapering.

In lingual view, the crown is very low: the ratio "length/height" of the crown varies between 1.55 and 2.25 in the material referred to this species. The main cusp A/a is not much higher than cusps B/b and C/c. Cusps B/b and C/c are usually subequal in size and it is therefore more difficult to distinguish the anterior and the posterior ends of the crown than in *Tricuspes tuebingensis* or in *Tricuspes sigogneauae*. They are more rounded and stocky than cusp A/a and their vertical axis can be somewhat divergent. The cusps are well separated from each other by deep notches. The accessory cusps D/d and E/e, when present, are incorporated in the cutting edge, as in *Tricuspes tuebingensis*, and not rejected on the anterior and posterior walls of the crown, as in *Tricuspes sigogneauae*.

There is no trace of cingulum or accessory cusp m, as in *Tricuspes tuebingensis*. The crown was apparently separated from the root by a constriction.

Wear facets are not always as well marked as in *Tricuspes sigogneauae* and it is therefore sometimes difficult to distinguish the lower from the upper molariform teeth. Wear erodes the upper teeth on their lingual and the lower teeth on their labial side.

In IRSNB R160 (lower molariform), the apices of cusps A, B and C are truncated by wear and have thus a bevel-edged aspect. Cusp A bears a second elliptical wear facet, from the apical facet to its base.

In IRSNB 28114/108 (upper molariform), the apices of cusps A, B and C are slightly blunt by small circular wear facets. The lingual side of the crown bears, below cusp b, a wide facet reminiscent of a contact facet with the contiguous tooth in the dental row.

The lingual side of IRSNB 28114/109 (upper molariform) has a very extensive, mat and slightly concave wear facet, extending from the anterior edge of cusp B to the anterior edge of cusp C and from the base of the crown to the apices of the cusps. A second wear facet, at the base of the posterior side of cusp C, can be inter-

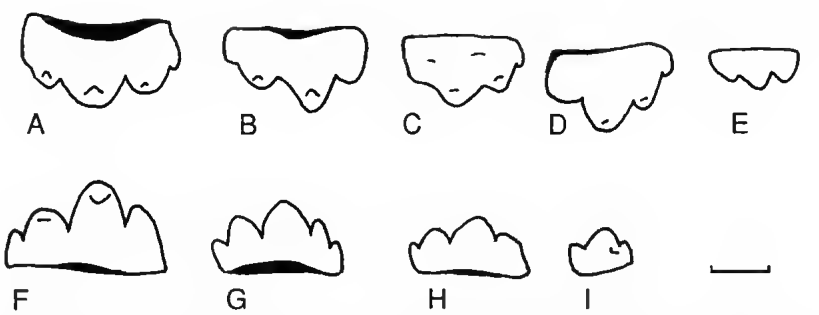

Fig. 8. — Outline of molariform teeth of *Tricuspes tapeinodon*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, IRSNB R161; **B**, IRSNB 28114/80; **C**, IRSNB 28114/108; **D**, MNHP SNP160W; **E**, IRSNB 28114/109; **F**, IRSNB 28114/106; **G**, IRSNB R160; **H**, IRSNB 28114/107; **I**, IRSNB 28114/35. Scale bar: 1 mm.

TABLE 3. — Measurements (in mm) of the molariform teeth of *Tricuspes tapeinodon*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown; **LL**, lower left; **LR**, lower right; **UL**, upper left; **UR**, upper right.

Number	Position	Lc	Wc	Hc	Lc / Wc	Root	Cusps
IRSNB 28114/35	? LL	1.15	0.4	0.74	2.87	-	3
IRSNB 28114/107	? LL	2.28	0.6	1.02	3.8	-	+ 3
IRSNB 28114/106	LR	2.87	0.85	1.5	3.38	-	3 +
IRSNB R160	? LR	2.27	0.7	1.33	3.24	-	+ 3 +
IRSNB 28114/80	UL	2.62	0.82	1.46	3.19	-	3 +
IRSNB 28114/827	UL	-	0.98	1.5	-	-	+ 3 (?)
MNHP SNP160W	UL	>2.3	0.72	-	>3.26	-	+ 3 (?)
IRSNB R161	UR	2.83	0.9	1.62	3.14	-	+ 3 +
IRSNB 28114/108	UR	2.15	0.95	1.27	2.26	-	3 +
IRSNB 28114/109	UR	1.65	0.67	0.75	2.46	-	3

preted as a contact facet with the contiguous posterior tooth in the dental row. It seems, therefore, that the teeth of the same row were aligned, which permits one-to-one occlusion between teeth of the opposite rows.

The labial side of IRSNB 28114/106 (lower molariform) bears three wear facets. The first one erodes the posterior edge of cusp b and the anterior edge of cusp a. The second one is continuous on the posterior edge of cusp a and on the anterior edge of cusp c. The third facet affects the posterior edge of cusp c and the anterior edge of cusp d.

Root

The root is not preserved in the molariform tooth referred to *Tricuspes tapeinodon*.

DISCUSSION

Figure 9 compares the distribution of the length (x axis, in Ln) and of the width (y axis, in Ln) of the molariform teeth in the three species recognized in the genus *Tricuspes*. It appears that *T. tapeinodon* has, in average, proportionally narrower dental crowns than *T. sigogneauae*. This result can be considered as significant because

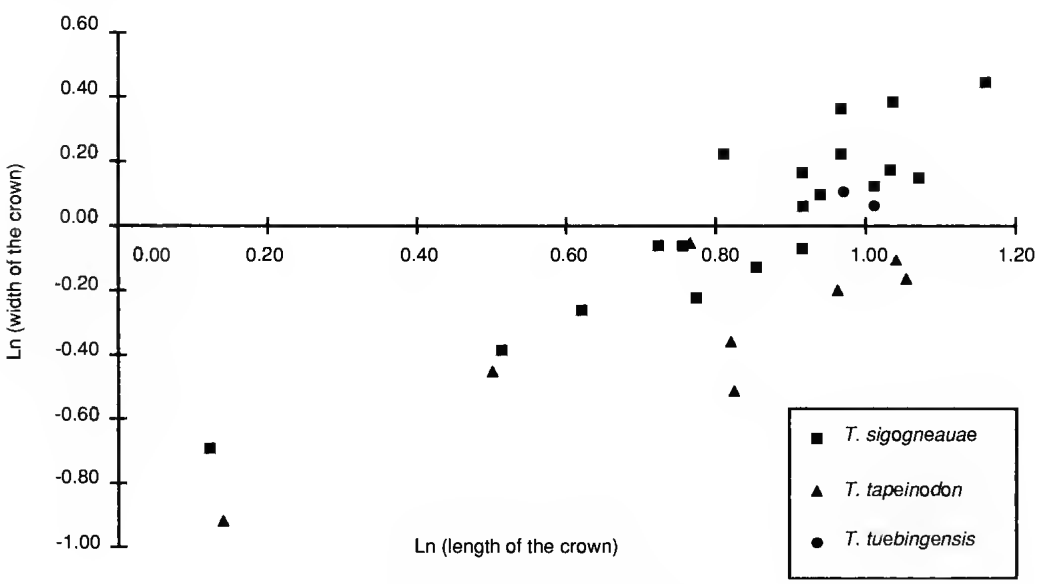

FIG. 9. — Dispersion diagram of the molariform teeth in *Tricuspes*.

Pearson's correlation coefficients are sufficiently high: r = 0.91 and 0.84, respectively in *T. sigogneauae* and *T. tapeinodon*. The allometry coefficient, estimated by Teissier's (1948) formula differs between these species (b = 1.16 in *T. sigogneauae* and 0.9 in *T. tapeinodon*), which confirms their taxonomic distinction. There is no evidence, at our present state of knowledge, to support a generic distinction of *Tricuspes tapeinodon*.

Genus *Meurthodon*
Sigogneau-Russell *et* Hahn, 1994

Meurthodon Sigogneau-Russell *et* Hahn, 1994: 212.

TYPE SPECIES. — *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994.

DIAGNOSIS. — As for the only currently recognized species *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994.

Meurthodon gallicus
Sigogneau-Russell *et* Hahn, 1994
(Figs 10, 11)

Meurthodon gallicus Sigogneau-Russell *et* Hahn, 1994: 212, figs 10.11. – Hahn *et al.* 1994: 142, fig. 2f.

Tricuspes sp. indet. – Hahn *et al.* 1994: *partim* 154, fig. 15.

"*Dent d'aspect mammalien*" (Russell *et al.* 1976: 377, pl. 1, figs 1-3).
"... probably representative of a cynodont reptile..." (Clemens 1979: 11).
"Advanced mammal-like reptile" (Clemens 1980: 62).
"French mammal (?)" (Gow 1980: 480, fig. 10).

HOLOTYPE. — MNHP SNP1W.

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

STRATUM TYPICUM. — "Rhaetian" sandstones. Upper Triassic.

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: MNHP SNP1W, IRSNB R162, IRSNB R163, IRSNB 281141/5, IRSNB 28114/17, IRSNB 28114/40, IRSNB 28114/45, IRSNB 28114/56, IRSNB 28114/746, IRSNB 28114/754, IRSNB 28114/814, IRSNB 28114/902, IRSNB 28114/993, MNHP SNP51DD, MNHP SNP64W, MNHP SNP115W, MNHP SNP200W, MNHP SNP210W, MNHP SNP514W.

DIAGNOSIS. — Crown of postcanine teeth asymmetrical and tetracuspid. The second cusp is always the largest and the first cusp is usually the smallest. The three posterior cusps are clearly inclined backwards. Small erratic cingular elements on some teeth. Crown

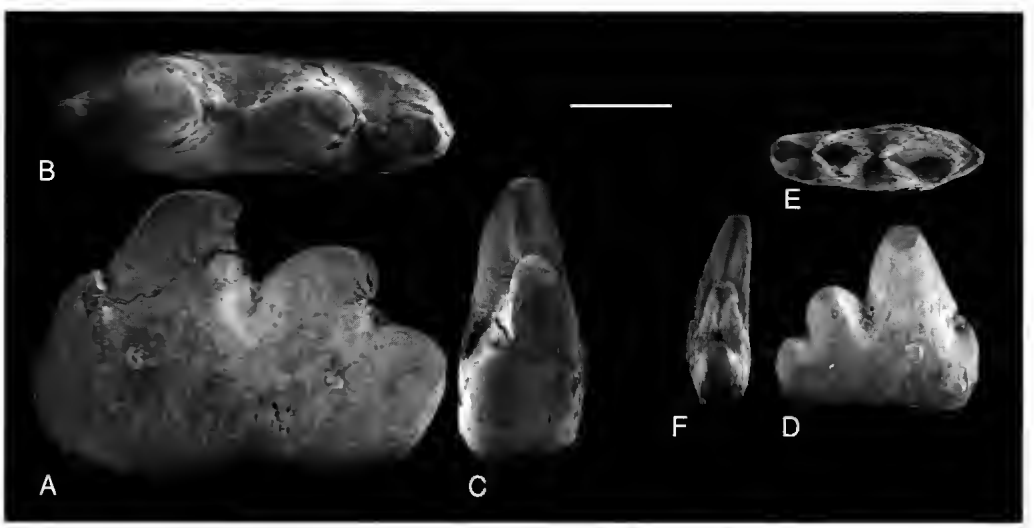

FIG. 10. — Postcanine teeth of *Meurthodon gallicus*, from the Late Triassic of Saint-Nicolas-de-Port. **A-C**, IRSNB R162, lower postcanine; **A**, lateral view; **B**, occlusal view; **C** posterior view. **D-F**, IRSNB R163, upper postcaine; **D**, lateral view; **E**, occlusal view; **F**, posterior view. Scale bar: 1 mm.

clearly separated from the root by a sulcus. Roots completely subdivided and fully separated on the distal three quarters of their length.

Description

Preliminary remark

Until now, the holotype (MNHP SNP1W) was the only known specimen of *Meurthodon gallicus*. The original description of this tooth (Russell *et al.* 1976) is particularly detailed. Therefore, the following description points only to differential characters observed in new material referred to this species.

Measurements

The measurements taken on the postcanine teeth of *Meurthodon gallicus* are shown in table 4.

General characters of the crown

The crown is tetracuspid and the cusps are very compressed labio-lingually. The second cusp is always the highest. Its is flanked by a small anterior cusp and by two posterior cusps of decreasing sizes. The three posterior cusps slope backwards. The crowns of some teeth (IRSNB 28114/005, IRSNB 28114/902) are proportionally less long, but higher than in MNHP SNP1W. This feature can reflect the relative position of the tooth in the jaw: the most slender teeth have a pronounced premolariform aspect.

First cusp

The first cusp is always quite small. Its axis is nearly perfectly vertical, but can sometimes slope backwards (IRSNB 28114/40). It is usually adjacent to the second cusp, but can be separated from it by a more or less deep groove. It is sometimes slightly displaced towards the lingual side of the crown (IRSNB 28114/5, IRSNB R163, IRSNB 28114/814, MNHN SNP115W). The first cusp of MNHP SNP1W, IRSNB 28114/40, IRSNB 28114/056, IRSNB R162, MNHP SNP64W and MNHP SNP210W bears, on its anterior lingual side, a well marked flat triangular facet. This suggests a contact between contiguous teeth and thus, a mesio-distal overlapping of the teeth (Russell *et al.* 1976). In IRSNB R162, a tiny accessory cusp, at the base of the labial side of the first cusp, is prolonged backwards by a brief ridge.

Second cusp

The second cusp is always by far the highest. Its labial side is more convex than its lingual side. Its apex is rounded. It slopes backwards: its vertical axis forms an angle of 60° to 70° with the horizontal axis of the crown. Its posterior margin is always less oblique than its anterior margin. Both are made thinner, cutting, usually pinched at the base and more rounded at the top. The cusp can be slightly curved towards the lingual side of the crown (IRSNB 28114/5, IRSNB 28114/17, IRSNB R163). At the level of the junction with the third cusp, both the labial and the lingual sides of the crown bear a concave dimple. The labial one is always better marked.

Third cusp

The third cusp is nearly identical to the second. It is usually still more inclined backwards (MNHP SNP1W, IRSNB R163, IRSNB 28114/40, IRSNB 28114/56, IRSNB 28114/902). It is always smaller than the second cusp and higher than the first and the fourth. Its anterior and posterior margins are cutting, too, particularly at their base. Its labial and lingual sides also bear small facets, at the level of the junction with the fourth cusp.

Fourth cusp

The fourth cusp is usually higher than the first one (MNHP SNP1W, IRSNB 28114/5, IRSNB 28114/17, IRSNB R163, IRSNB 28114/45, IRSNB 28114/56, MNHP SNP64W, MNHNP SNP210W), but can sometimes be somewhat smaller (IRSNB 28114/902, IRSNB 28114/993, MNHP SNP200W). It is always less inclined backwards than the third: its slope is approximately the same than that of the second cusp. Its apex is usually more sharp-pointed than that of the second and the third cusps. Its anterior margin is sharper than its posterior margin, which participates in the posterior border of the crown. The posterior border of the fourth cusp bears, in IRSNB 28114/5 and IRSNB R163, a well marked triangular mai facet, probably corresponding to the overlapping area with the contiguous posterior tooth in the dental series. In IRSNB 28114/040, a posterior swelling forms a tiny posterior accessory cusp.

Base of the crown

The base of the crown is distinctly constricted by a sulcus separating it from the root. Under the cusps, the labial side of the crown is usually convex antero-posteriorly; the lingual side is flat to slightly concave. The labial side sometimes presents a concavity between the second and the third cusp (MNHP SNP 1W, IRSNB 28114/5, IRSNB 28114/56). Between these cusps, the base of the lingual side of the crown bears a dimple in continuity with the separation line of the roots.

The labial side of IRSNB R162 bears, under the junction between the third and the fourth cusp, a small swelling which can be interpreted as the rough shape of a cingulum. If the orientation proposed above is correct, the presence of cingular elements on the labial side should indicate, by analogy with the Morganucodontidae, that this tooth is an upper postcanine. The presence of wear facets on the labial side of the cusps contradicts this interpretation (see below). Such a swelling can be observed on the lingual side of IRSNB 28114/17, under the junction between

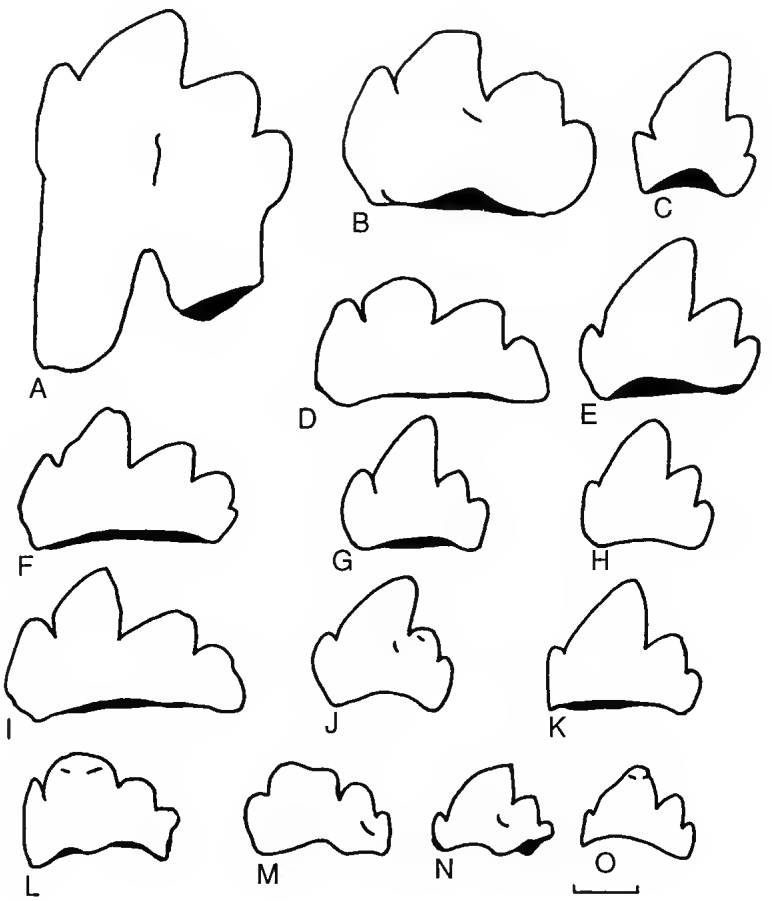

FIG. 11. — Outline of postcanine teeth of *Meurthodon gallicus*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, MNHP SNP1W; **B**, IRSNB R162 (lower postcanine); **C**, IRSNB 28114/902; **D**, IRSNB 28114/40; **E**, MNHP SNP210W; **F**, MNHP SNP64W; **G**, IRSNB 28114/993; **H**, IRSNB R163 (upper postcanine); **I**, IRSNB 28114/746; **J**, IRSNB 28114/17 (lower postcanine); **K**, MNHP SNP514W; **L**, IRSNB 28114/56 (lower postcanine); **M**, IRSNB 28114/45 (lower postcanine); **N**, MNHP SNP51DD; **O**, MNHP SNP20W. Scale bar: 1 mm.

the second and the third cusp. With the lingual dimple between the second and the third cusp, this swelling delimits a small lingual basin. A tiny accessory cusp can be observed on the lingual side of IRSNB 28114/5, under the junction between the second and the third cusp. These last two teeth, which present cingular elements only on their lingual side, are therefore probably lower postcanines.

Wear facets

Russell *et al.* (1976) did not observe clearly defined wear facets in MNHP SNP1W. The flat anterior facet on the first cusp is nevertheless interpreted, as mentioned above, as a contact area with the contiguous tooth. The flatter upper half of the fourth cusp is similarly regarded as a contact area with the posterior tooth. These facets indicate that the teeth of the same row were aligned, which is an important prerequisite to one-to-one occlusion (Crompton & Luo 1993; Luo 1994). However, several other teeth present clearly defined wear facets.

Two elongated, semielliptical and concave facets are present on the labial side of the second and third cusps, in IRSNB 28114/5. The facet extends nearly as far as the base of the second cusp. If the orientation proposed is correct, this tooth is therefore a lower postcanine.

In IRSNB 28114/56, wear facets are also located on the lingual side of the second and third cusps. The first facet truncates the top of the second cusp. The second facet is long and oblique forwards: it reaches the base of the third cusp. This tooth is therefore probably a lower postcanine.

In IRSNB 28114/17, the labial side of the apex is truncated by an elliptical wear facet, which confirms its attribution to the lower dental series.

In IRSNB R162, a wear facet extends on the anterior side of the apex of the second cusp, replacing its natural cutting edge by a narrow, flat and elongated facet, and, on the its labial side, forming a small triangular area. The interpretation of this tooth is difficult: both the cingular elements and the wear facet are present on the same side and the cusps are not curved. If the orientation of this tooth is correct, it is thus a lower postcanine with tiny external cingular elements.

MNHP SNP 115W has been identified by Hahn *et al.* (1994, fig. 15) as *Tricuspes* sp. In fact, it presents all the diagnostic characters of *Meurthodon gallicus*. The labial side of its last three cusps possesses well marked wear facets. Thus, it is probably a lower postcanine.

MNHP SNP 200W also possesses a well marked elongated wear facet on the labial side of its second cusp, which permits its attribution to the lower dental series.

Two wear facets can be observed on the lingual side of IRSNB R163. The first, triangular in shape, is located at the apex of the second cusp; the second facet is elongated on the third cusp. This is therefore probably an upper postcanine.

Roots

The roots can only be observed on the holotype and have been described in detail by Russell *et al.* (1976).

Discussion

Russell *et al.* (1976) discuss in detail the affinities of the holotype MNHP SNP1W and emphasize the close resemblance of this tooth with those of the Late Triassic cynodont *Therioherpeton cargnini* Bonaparte *et* Cabrera, 1975 and with those of *Sinoconodon rigneyi* Patterson *et* Olson, 1961. The latter genus is now clearly recognized as a true mammal, forming the sister-group of a monophyletic taxon that includes all the other

Table 4. — Measurements (in mm) of the postcanine teeth of *Meurthodon gallicus*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown.

Number	Lc	Wc	Hc	Lc/Wc
MNHP SNP1W	4.25	1.32	3.05	3.22
IRSNB 28114/005	2.17	0.8	> 2	2.71
IRSNB 28114/017	2.32	0.8	2.23	2.9
IRSNB R163	2.25	0.72	2.12	3.12
IRSNB 28114/040	3.9	1.1	> 2.1	3.54
IRSNB 28114/045	2.42	0.9	-	2.69
IRSNB 28114/056	2.6	0.87	>1.85	2.99
IRSNB R162	4.25	1.35	2.9	3.15
IRSNB 28114/746	3.95	1.07	2.4	1.65
IRSNB 28114/754	2.98	0.9	-	3.31
IRSNB 28114/902	2	0.88	2.37	2.27
IRSNB 28114/993	2.48	-	2.1	-
MNHP SNP64W	3.53	0.97	2.25	3.64
MNHP SNP200W	1.85	0.8	1.43	2.31
MNHP SNP210W	3.02	1.01	2.7	2.99
MNHP SNP514W	2.67	0.89	2.17	3

mammals (Crompton & Luo 1993; Wible & Hopson 1993; Lucas & Luo 1993; Luo 1994). Sigogneau-Russell & Hahn (1994) group *Therioherpeton* and *Meurthodon* within the family Therioherpetidae. This family is thought to form the sister-group of the Dromatheriidae. Hahn *et al.* (1994) gather both genera within the family Dromatheriidae.

The new specimens discovered in Saint-Nicolas-de-Port permit a better understanding of the dental variability in *Meurthodon*. The postcanine teeth of *Meurthodon* are compared in detail with those of *Therioherpeton* and *Sinoconodon*, in order to clarify the affinities of the genus:

1. The presence of wear facets on the labial side or on the lingual side of the crowns attests that the material referred to *Meurthodon* includes upper and lower postcanines morphologically identical. This seems to be a usual character in the Dromatheriidae. The upper and lower postcanines seem also very similar in *Sinoconodon*. In *Therioherpeton*, the upper and the lower postcanines seem to be constructed following the same plan, but the poor preservation of the material prevents more precise comparisons.

2. In *Sinoconodon*, postcanine teeth lack differenciation into premolariform and molariform teeth (Crompton & Sun 1985). In adult dental formula, the single canine is separated from the first postcanine by a long diastema (Patterson & Olson 1961). The anterior postcanines are lost without replacement, resulting in an increasingly large postcanine diastema during ontogeny. At least two postcanines are added to the posterior end of the tooth row and at least one postcanine was replaced in older specimens (Crompton & Luo 1993). In *Therioherpeton*, the crowns of the anterior postcanines are not preserved, but the size of their alveolae are smaller than in the posterior molariform teeth. Their postcanine dentition was thus probably subdivided into premolariform and molariform teeth. Bonaparte & Barberena (1975) observed an alternate tooth replacement in this genus. In *Meurthodon*, only isolated teeth have been discovered: this prevents the identification of premolariform teeth in this genus (see below). Nevertheless, some teeth have a more slender aspect than others: this can reflect their relative position in the dental series. The tooth replacement pattern is unknown in *Meurthodon*.

3. In *Meurthodon*, the roots of molariform teeth are fully separated on three quarters of their length, but fused proximally below the crown. In *Therioherpeton*, they are separated on the whole length, but connected by a thin sheet of dentine. In *Sinoconodon*, like in *Meurthodon*, the postcanine roots are divided only along their distal parts (Luo 1994, fig. 6.6).

4. In *Meurthodon*, the presence of small facets on the anterior and posterior parts of the crown reveals the contact between contiguous postcanines. In *Therioherpeton*, the distal postcanines have an oblique implantation, like in the Tritheledontidae: the anterior margin of the distal postcanine is placed antero-lingually to the posterior margin of the mesial tooth. The adjacent postcanines of *Sinoconodon* do not interlock with one another (Crompton & Luo 1993).

5. The postcanines of *Meurthodon* show wear facets. They do not seem constant, like in the Morganucodontidae or later mammals, indicating that the relations between lower and upper postcanines were not yet clearly defined. A stronger wear seems to affect the cusps of *Therioherpeton* (see Bonaparte & Barberena 1975). In *Sinoconodon*, the postcanine crowns lack wear facets, which is probably correlated to the absence of one-to-one alignment of the corresponding upper and lower molariforms (Crompton & Luo 1993; Luo 1994).

6. Tiny and very inconstant cingular elements can be observed on *Meurthodon* postcanines. *Therioherpeton* lacks cingulum or cingular accessory cusps. Some of the best preserved postcanines of *Sinoconodon* possess a faint labial cingulum on the uppers and a more distinct one on the posterolingual surface of the lowers (Crompton & Sun 1985; Crompton & Luo 1993).

7. In these three genera, the crown is laterally compressed and fundamentally tetracuspid: the second cusp is the highest and the decreasing size of the distal cusps is regular. The cusps are proportionally higher and better defined in *Meurthodon* than in *Therioherpeton*, but this may be a result of a stronger wear in the latter genus (Sigogneau-Russell & Hahn 1994). The cusps do

not present backwards slope in *Therioherpeton*. The first cusp is independant from the second and the last two cusps are closer side by side than in *Meurthodon* (Russell *et al.* 1976). A fifth anterior accessory cusp can be observed on some postcanines in *Sinoconodon* (see Patterson & Olson 1961; Crompton & Sun 1985). The first cusp is usually better separated from the second than in *Meurthodon*. The last three cusps are also usually less inclined.

Comparisons with the advanced cynodont *Therioherpeton* and the primitive mammal *Sinoconodon*, whose dentition is most similar, reveal that the postcanine teeth of *Meurthodon* present a mosaic of plesiomorphic (low development of cingular elements) and apomorphic (better separated roots, wear facets, ? contacts between adjacent postcanines) characters. As this taxon is currently known only by its postcanine teeth, it is not possible to decide whether *Meurthodon* is a very advanced cynodont or a true early mammal. Waiting for further evidence, this genus is provisionally and questionably classified whithin the Dromatheriidae, as suggested by Hahn *et al.* (1994). This seems the most conservative course, in the present state of knowledge.
Morphometrically, the dispersion diagram of the postcanine teeth in *Meurthodon gallicus* shows a negative allometry between the width and the length of the crowns (Fig. 12): the allometry coefficient b, calculated according Tessier's (1948) formula, is 0.63. Pearson's correlation coefficient is high (r = 0.89) and this result can therefore be regarded as correct. This negative allometry reflects the cutting function of the postcanine teeth in *Meurthodon*. The correlation between the length and the height of the postcanine crowns is too low (r = 0.63) to permit a correct estimation of the allometry coefficient between these variables.

CYNODONTIA INCERTAE SEDIS
Genus *Hahnia* n.g.

TYPE SPECIES. — *Hahnia obliqua* n.sp.

DERIVATIO NOMINIS. — Dedicaced to Prof. Dr. G. Hahn, for his contribution to the knowledge of Late Triassic cynodonts and early mammals from Lorraine.

DIAGNOSIS. — As for the only currently recognized species *Hahnia obliqua* n.sp.

DISCUSSION
See under *Hahnia obliqua* n.sp.

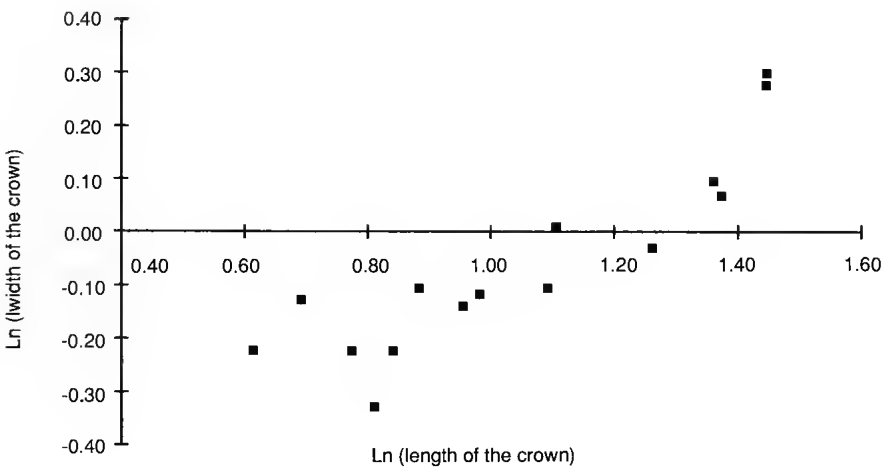

FIG. 12. — Dispersion diagram of the postcanine teeth in *Meurthodon*.

Hahnia obliqua n.sp.
(Fig. 13)

HOLOTYPE. — IRSNB R164, a left upper postcanine, with its root nearly completely preserved.

PARATYPES. — MNHP SNP50DD, a complete lower right postcanine; IRSNB 28114/102, MNHP SNP23 and MNHP SNP57, crowns without roots of upper postcanines.

DERIVATIO NOMINIS. — *obliquus, -a, -um* (lat.) = oblique. Refers to the vertical axis of the crown, inclined backwards.

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

STRATUM TYPICUM. — "Rhaetian" sandstones. Upper Triassic.

DIAGNOSIS. — Ratio "length/width" of the crown > 3. Vertical axis of the crown inclined backwards. Main cusp slightly curved towards the lingual side. Labial side of the crown clearly more convex than the lingual side. Elongated wear facets along the anterior and posterior cutting edges, on the upper postcanines. Base of the crown not constricted. Root semielliptical in outline, 1.5 to 2 times as high as the crown. Pulpal canal narrow and elliptical in outline.

DESCRIPTION

Measurements

Table 5 shows the measurements taken on the postcanine teeth of *Hahnia obliqua* from Saint-Nicolas-de-Port.

Crown

The crown is tricuspid and the enamel, perfectly smooth. In occlusal view, the crown is very compressed labio-lingually: 3 < ratio "length/width" of the crown < 3.65. The labial side is convex antero-posteriorly, while the lingual side is slightly concave. As in *Pseudotriconodon*, the three cusps are perfectly aligned on the mesio-distal axis of the crown. Nevertheless, the edge is not as sharp as in the latter genus. On the upper postcanines, the edge is particularly blunt between the main cusp and the mesial cusp. The apex of the main cusp is rejected to the lingual side.

In anterior view, the main cusp is not perfectly straight, as in *Pseudotriconodon*, but curved towards the lingual side, particularly in its upper portion.

In lingual view, the vertical axis of the crown is inclined backwards, forming an angle of approximately 15° with the vertical axis of the root. The

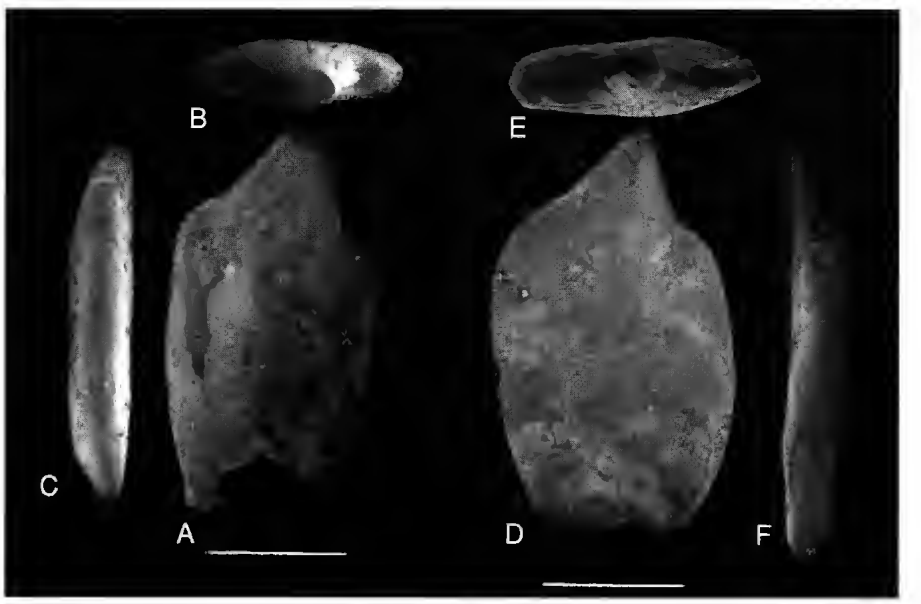

FIG. 13. — Postcanine teeth of *Hahnia obliqua*, from the Late Triassic of Saint-Nicolas-de-Port. **A-C**, IRSNB R164, upper postcanine; **A**, lateral view; **B**, occlusal view; **C**, anterior view. **D-F**, MNHP SNP50DD, lower postcanine; **D**, lateral view; **E**, occlusal view; **F**, posterior view. Scale bar: 1 mm.

TABLE 5. — Measurements (in mm) of the postcanine teeth of *Hahnia obliqua*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown; **Hr**, height of the root.

Number	Lc	Wc	Hc	Hr
IRSNB R164	1.6	0.45	1.15	2.1
IRSNB 28114/102	1.25	0.4	> 1.2	-
MNHP SNP50DD	1.82	0.5	1.25	1.9
MNHP SNP23	2.3	0.75	-	-

main cusp has a triangular outline; its anterior and posterior edges are straight, but its apex is always somewhat blunt. It is flanked by a pair of very blunt triangular accessory cusps. These are not well separated from the main cusp. Because of the backwards slope of the crown, the distal accessory cusp seems lower than the mesial cusp.
In the upper postcanines, a well marked wear facet runs along the posterior edge, on the lingual side of the main cusp. This looks like an elongated, very narrow and mat surface. In IRSNB 28114/102 and MNHP SNP23, a second wear facet is present on the anterior edge of the main cusp; it is less marked and less long (stopping below the apex of the main cusp) than the first one. This facet is absent from IRSNB R164, but the anterior edge of the main cusp is very blunt. A third small facet is present on the lingual side of the apex of the main cusp. In MNHP SNP50DD, identified as a lower postcanine, a small wear facet is present on the labial side of the main cusp, in the middle of the anterior edge.
There is no constriction between the crown and the root.

Root
The root is nearly complete in IRSNB R164 and complete in MNHP SNP50DD. In IRSNB R164, the root is nearly 2 times as high as the crown; in MNHN SNP50DD, the ratio "height of the root/height of the crown" = 1.5. In basal view, it is very compressed labio-lingually. Its labial side is slightly convex antero-posteriorly; the upper portion of its lingual side is flat and the lower portion is slightly concave. The pulpal foramen is small and elliptical in outline. It does not show any evidence of bipartition.
In lateral view, the root has a semi-elliptical outline. It gradually and symmetrically gets narrow towards the tip.

DISCUSSION
By their general morphology, these teeth are reminiscent of the small carnivorous cynodonts from the Upper Triassic: the crown is tricuspid, smooth, very narrow labio-lingually, with a cutting edge and without cingulum; the root is high and semielliptical in shape (Hahn *et al.* 1984). The affinities with the different families of Triassic carnivorous cynodonts are nevertheless difficult to establish. The main characters of the postcanine teeth in these families are reviewed below and compared with those of *Hahnia obliqua*.

Thrinaxodontidae
(Late Permian of South Africa and Russia, Early Triassic of South Africa)
In contrast with *Hahnia obliqua*, the postcanine teeth of the Thrinaxodontidae are not strictly sectorial, but possess an internal cingulum with small cusps (Hopson & Kitching 1972; Battail 1991). The lingual side of the upper postcanines does not bear marked wear facets.

Galesauridae
(Late Permian and Early Triassic of South Africa)
Like in *Hahnia*, the postcanine teeth of the Galesauridae are devoid of cingulum. Nevertheless, in *Cynosaurus* Schmidt, 1927, they are less compressed labio-lingually and the anterior accessory cusp is less detached. In *Galesaurus* Owen, 1860, the postcanines are very compressed labio-lingually, but, in contrast with *Hahnia*, the main cusp is very curved backwards and there is no anterior accessory cusp (Battail 1991). The teeth do not bear marked wear facets (Crompton 1972).

Cynognathidae
(Early Triassic and Early Middle Triassic of South Africa and South America)
The Cynognathidae form a monogeneric family (Battail 1991). The postcanine teeth of *Cynognathus* Seeley, 1895 are similar to those of *Hahnia*: the crown is very compressed labio-lingually, devoid of cingulum and formed by a

high central cusp flanked by several accessory cusps perfectly aligned antero-posteriorly, forming a cutting edge. The vertical axis of the crown slopes backwards. The lingual side of the upper postcanines and the labial side of the lower postcanines bear marked wear facets (Crompton 1972). The root is undivided, but can be slightly depressed by a longitudinal furrow. Nevertheless, differences can be observed: in *Cynognathus*, the main cusp is curved backwards and somewhat serrated, especially in younger specimens.

Chiniquodontidae
(Lower Triassic of South Africa and Argentina, Middle Triassic of Tanzania, Argentina and Brazil, Upper Triassic of Argentina and Brazil)
In the Chiniquodontidae, the root of the postcanine teeth is never subdivided and can be separated from the crown by a well marked constriction. The presence of wear facets attests constant contacts between upper and lower postcanines, like in *Hahnia*. The crowns of postcanine teeth are strictly sectorial, following the complete disparition of the cingulum, in *Probelesodon lewisi* Romer, 1969 and *Probainognathus jenseni* Romer, 1970 (Battail 1989). The crowns of the postcanines, in *Probainognathus*, although very worn, are quite different from those of *Hahnia*: the main cusp, low and weakly developed, is flanked by an anterior and a posterior cusp poorly developed. The edge formed by these cusps is sinuous and devoid of sharp points. Only the most posterior postcanines are tricuspid in *Probelesodon:* the anterior accessory cusp is always very low and poorly separated from the main cusp. The latter is very curved backwards.

Tritheledontidae
(Late Triassic of Argentina, Early Jurassic of South Africa and the USA)
In the Tritheledontidae, the crowns of the postcanine teeth are always less compressed labio-lingually than in *Hahnia* and usually bear a cingulum (see Gow 1980).

Dromatheriidae
(Middle Triassic of Argentina, Late Triassic of Europe and the USA)
The postcanines of *Hahnia* are very similar to those of *Pseudotriconodon*: the crown is tricuspid, strictly sectorial without cingulum and very compressed labio-lingually; the cusps are perfectly aligned following the antero-posterior axis of the crown, forming a cutting edge; there is no constriction between the crown and the root; the root is semielliptical in outline and very compressed; the pulpal foramen is small and elliptical in outline. Marked wear facets are absent from *Pseudotriconodon* postcanines, but are observed in *Tricuspes*. The backwards slope of the crown is an uncommon feature in species currently referred to the Dromatheriidae. The only true diagnostical character of the family Dromatheriidae is the subdivision of the root in posterior postcanines. This feature is not present in the two complete teeth currently discovered in *Hahnia*. Nevertheless, the subdivision of the base of the root is very rare in the primitive Dromatheriidae *Pseudotriconodon*.

Small carnivorous cynodonts incertae sedis
(Late Triassic of Europe)
In *Lepagia* Hahn, Wild *et* Wouters, 1987 and *Gaumia* Hahn, Wild *et* Wouters, 1987, the postcanine teeth are fundamentally tricuspid and strictly sectorial, without cingulum, like in *Hahnia*. The root is always undivided. Contrary to *Hahnia*, the crown is never inclined backwards, the main cusp is not curved to the lingual side and does not bear marked wear facets, in both genera. Moreover, the crown is well separated from the root by a marked constriction.

In the current state of knowledge, the phylogenetical position of *Hahnia* within the infraorder Cynodontia seems difficult to establish. The structure of the postcanine teeth is similar to those of Cynognathidae, but the attribution to this family is very dubious, for want of true diagnostical characters in the postcanines; the *Cynognathus* Zone in South Africa (Spathian to Anisian, see Shishkin *et al.* 1995) and the Upper Triassic in Saint-Nicolas-de-Port are actually separated by a space of time of about 25 Ma. The postcanines of *Hahnia* resemble those of the Dromatheriidae, too, but there is no trace of bipartition of the root in the material currently

discovered. Waiting for further evidences, *Hahnia* is thus referred to Cynodontia *incertae sedis*.

Genus *Gaumia* Hahn, Wild *et* Wouters, 1987

Gaumia Hahn, Wild *et* Wouters, 1987: 11.

TYPE SPECIES. — *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987.

OTHER REFERRED SPECIES. — *Gaumia* ? *incisa* Hahn, Wild *et* Wouters, 1987.

DIAGNOSIS. — Crown of the postcanine teeth "triconodont", more or less narrow, with the labial and lingual sides nearly symmetrical. Axis of the crown perfectly vertical. Cusps not curved and more or less symmetrically arranged, the central cusp being the highest; cutting edge perfectly straight. No cingulum. Base of the crown constricted. Root triangular in outline and very high, at least 1.5 times as high as the crown. Tip of the root undivided; pulpal canal small and rounded to elliptical in outline.

Gaumia longiradicata Hahn, Wild *et* Wouters, 1987 (Figs 14, 15)

Gaumia longiradicata Hahn, Wild *et* Wouters, 1987: 12, pl. 4, fig. 1, pl. 5, fig. 1. – Battail 1991: 89. – Sigogneau-Russell & Hahn 1994: 206, fig. 10.10b.

HOLOTYPE. — IRSNB "R.M.35".

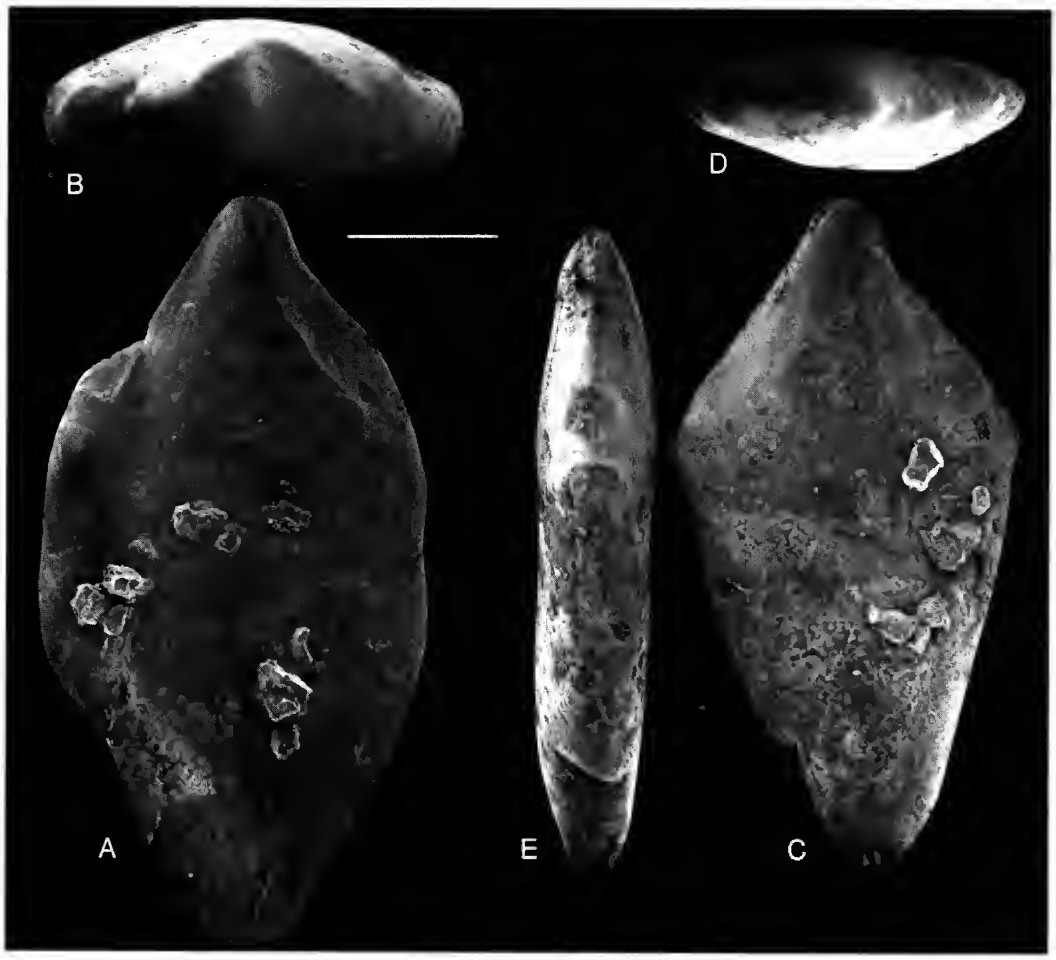

FIG. 14. — Postcanine teeth of *Gaumia longiradicata*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, **B**, IRSNB R165; **A**, lateral view; **B**, occlusal view. **C-E**, IRSNB R166; **C**, lateral view; **D** occlusal view; **E**, ? anterior view. Scale bar: 1 mm.

PARATYPE. — IRSNB "R.M.36".

LOCUS TYPICUS. — Side of the speedway E25-E411, at Habay-la-Vieille (Belgian Lorraine).

STRATUM TYPICUM. — Bone-bed "HLV-2", Grès de Mortinsart (Rhaetian, Upper Triassic).

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: IRSNB R165, IRSNB R166, IRSNB 28114/047, IRSNB 28114/055, IRSNB 28114/088, IRSNB 28114/090, IRSNB 28114/093, IRSNB 28114/646, IRSNB 28114/982, ? IRSNB 28114/771, MNHP SNP131L, MNHP SNP430W.

DIAGNOSIS. — Crown of postcanine teeth tri- to pentacuspid and relatively thick: 2.1 < ratio "length/width" of the crown < 2.75. First pair of accessory cusps (or median accessory cusps) not clearly individualized; second pair (lateral accessory cusp) more clearly separated. Smooth enamel on all cusps.

DESCRIPTION

Classification

The postcanine teeth of *Gaumia longiradicata* discovered in Saint-Nicolas-de-Port are classified according to the number and the position of the accessory cusps, as in *Pseudotriconodon wildi* (see above). The estimate of the number of accessory cusps is not always easy because these are usually weakly differenciated.

Measurements

The measurements taken on the postcanine teeth of *Gaumia longiradicata* discovered in Saint-Nicolas-de-Port are shown in table 6.

Crown

In *Gaumia longiradicata*, the postcanine crowns are perfectly smooth. In occlusal view, the crown is thicker than in *Pseudotriconodon wildi* or in *Gaumia* ? *incisa*: 2.1 < ratio "length/width" of the crown < 2.75. Both the labial and the lingual sides of the crown are convex at the level of the main cusp. The width of the crown progressively decreases towards the anterior and posterior ends. The cusps are perfectly aligned on the antero-posterior axis of the crown. Their edge, perfectly median and straight, is not as sharp as in *Pseudotriconodon wildi* or in *Gaumia* ? *incisa*.
In anterior view, the main cusp is perfectly

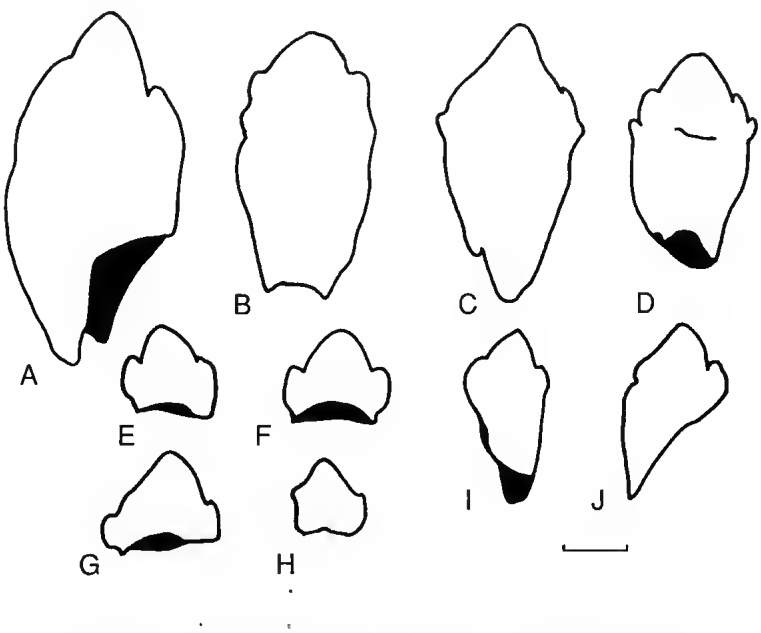

FIG. 15. — Outline of postcanine teeth of *Gaumia longiradicata*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, IRSNB R165; **B**, IRSNB 28114/47; **C**, IRSNB R166; **D**, IRSNB 28114/982; **E**, IRSNB 28114/90; **F**, IRSNB 28114/93; **G**, IRSNB 28114/55; **H**, IRSNB 28114/88; **I**, IRSNB 28114/646; **J**, MNHP SNP131L. Scale bar: 1 mm.

TABLE 6. — Measurements (in mm) of the postcanine teeth of *Gaumia longiradicata*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown; **Hr**, height of the root. For the signification of the groups, see text.

Group	Number	Lc	Wc	Hc	Hr	Lc/Wc	Hr/Hc
I	IRSNB 28114/047	1.95	0.75	1.4	2.75	2.6	1.96
	IRSNB 28114/088	1.2	0.5	0.85	-	2.4	-
	IRSNB 28114/090	1.5	0.65	1.2	-	2.31	-
	IRSNB 28114/093	1.7	0.8	1.3	-	2.12	-
	IRSNB 28114/646	1.9	0.7	1.1	>1.6	2.71	>1.5
	MNHP SNP131L	1.67	0.61	? 1.18	-	2.73	-
	MNHP SNP430W	1.32	0.53	-	-	2.49	-
?	IRSNB R165	1.6	0.71	2	3.3	2.26	1.65
II	IRSNB 28114/055	1.9	0.75	1.8	-	2.53	-
IV	IRSNB 28114/982	1.95	0.75	1.5	>1.9	2.6	>1.27
IV ?	IRSNB R166	2.3	0.9	1.8	2.65	2.56	1.47

straight, not curved to the lingual side of the crown.

In lateral view, the main cusp has a triangular outline and is specially broad: its base occupies nearly the full length of the crown. Its borders are straight to slightly concave. Its apex is less sharp than in *Pseudotriconodon wildi*. The median pair of accessory cusps is set along the lower third of the main cusp. These are not very developed and always very blunt: they can be separated from the main cusp by an indentation which is not very deep (IRSNB 28114/093, IRSNB R165), or can be presented as a vague undulation of the edges of the main cusp (IRSNB 28114/047, IRSNB 28114/646). When the lateral accessory cusps are present, they are set at the base of the crown, quite anteriorly and/or posteriorly. These lateral accessory cusps are very small (less than one tenth of the height of the main cusp), narrow, but better differenciated than the median accessory cusps.

Wear is apical and very erratic, as in *Pseudotriconodon wildi*. It does not form clearly marked wear facets. The crown and the root are

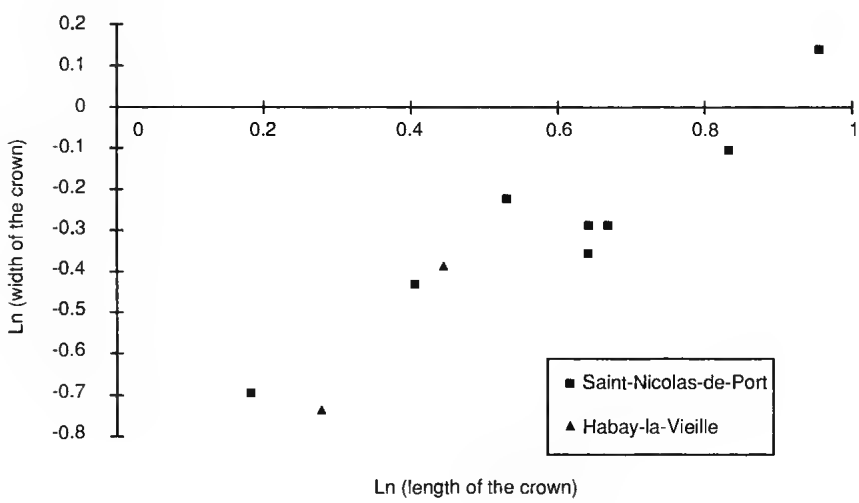

FIG. 16. — Dispersion diagram of the postcanine teeth in *Gaumia longiradicata*.

clearly separated by a constriction.

Root

The root is preserved in IRSNB 28114/047, IRSNB 28114/646, IRSNB R165, IRSNB 28114/982, IRSNB R166 and MNHP SNP131L. In anterior view, the root is less narrow and thus, more robust than in *Pseudotriconodon wildi*. This explains the higher proportion of preserved roots in *Gaumia longiradicata*. The root is much higher than the crown: the ratio "height of the root/height of the crown" varies between 1.47 (IRSNB R166) and 1.96 (IRSNB 28114/047). It has, in lateral view, a subtriangular outline: its length lessens quickly and symmetrically towards the tip. Its anterior and posterior borders are straight (IRSNB 28114/913) to slightly convex (IRSNB 28114/047, IRSNB R165, IRSNB 28114/982). The tip of the root is rounded and pierced by a small rounded to elliptical pulpal foramen: this pulpal canal is never double, as in *Pseudotriconodon wildi*.

In IRSNB R166, the anterior (?) border of the root is naturally truncated at the level of its lower third. A small lunulate foramen is visible at the level of the truncature. As this feature can be observed in only one specimen, it is not possible to know whether this represents a second pulpal foramen or more simply an isolated anomaly of the root.

DISCUSSION

Gaumia resembles *Pseudotriconodon* in the general aspect of the crown of its postcanines. However, the base of the crown is constricted and the root is higher and subtriangular in outline. The absence of bipartition of the root suggests that *Gaumia* is not a member of the family Dromatheriidae. The presence of a second pulpal foramen in IRSNB R166 needs to be confirmed by future discovery of additional specimens showing this feature. The absence of true apomorphies in the postcanine dentition of *Gaumia* leads to consider this genus as a Cynodontia *incertae sedis* (see Hahn *et al.* 1987; Battail 1991).

The postcanine teeth discovered in Saint-Nicolas-de-Port can be referred to the species *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987: their crown is relatively thick and the enamel is perfectly smooth on all cusps. These teeth cannot be morphometrically distinguished from the type material discovered in Habay-la-Vieille (Fig. 16). In this species, the length and the width of the crown are isometrical (b = 0.99; r = 0.94). The dental crowns referred to *Gaumia* ? *incisa* Hahn, Wild *et* Wouters, 1987 are significantly narrower and enamel ridges are present on the lingual side of the main cusp. Peyer (1956, pl. 9, figs 18, 27, 34, 44 and 47) describes several teeth from the Upper Triassic of Hallau (Switzerland) that can be referred to the genus *Gaumia*. They are characterized by few indistinct enamel ridges on both the lingual and the labial sides of the main cusp: they probably belong to a new undescribed species (Sigogneau-Russell & Hahn 1994).

Genus *Lepagia* Hahn, Wild *et* Wouters, 1987

Lepagia Hahn *et al.*, 1987: 5.

TYPE SPECIES. — *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987.

DIAGNOSIS. — As for the only currently recognized species, *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987.

Lepagia gaumensis
Hahn, Wild *et* Wouters, 1987
(Figs 17, 18)

Lepagia gaumensis Hahn *et al.*, 1987: 7, fig. 2, pl. 1, fig. 1, pl. 2, figs 1, 2. – Battail 1991: 89. – Sigogneau-Russell & Hahn 1994: 206, fig. 10, 10a.

"*Zähne von wahrscheinlich synapsiden Reptilien, Gruppe a*" (Peyer 1956: 56, *partim*, pl. 5, fig. 66, pl. 10, fig. 68).

"*Zahn eines synapsiden Reptiles*" (Kindlimann 1984: 3, fig. 4).

HOLOTYPE. — IRSNB "R.M.28".

PARATYPES. — IRSNB "R.M.29" and IRSNB "R.M.30".

LOCUS TYPICUS. — Side of the speedway E25-E411, at Habay-la-Vieille (Belgian Lorraine).

STRATUM TYPICUM. — Bone-bed "HLV-2", Grès de Mortinsart (Rhaetian, Upper Triassic).

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: IRSNB R167, IRSNB 28114/051, ? IRSNB 28114/104.

DIAGNOSIS. — Crown of the postcanine teeth long, narrow (2.5 < ratio "length/width" of the crown" < 3,7) and tricuspid to pentacuspid; labial and lingual sides of the crown slightly convex and nearly parallel; cutting edge of the cusps perfectly straight. Crown asymmetrical in lateral view. Axis of the crown perfectly vertical. No cingulum. Base of the crown very constricted. The root, nearly rectangular in lateral view and subequal in height to the crown, does not taper distally. Pulpal canal restricted to a long and narrow slit. Horizontal ramus of the mandible very low. Splenial very thin, extending halfway up on the lingual side of the dentary.

DESCRIPTION

Orientation

As in *Pseudotriconodon wildi* (see above).

Measurements

Measurements taken on the postcanine teeth of *Lepagia gaumensis* discovered in Saint-Nicolas-de-Port are shown in table 7.

Crown

The crown is perfectly smooth in IRSNB 28114/051 and IRSNB R167; some indistinct enamel tidges are present on the labial side of the apex of the main cusp, in IRSNB 28114/104. In occlusal view, the crown is rather long and narrow: the ratio "length/width" of the crown varies between 2.5 and 3.5 in the teeth discovered in Saint-Nicolas-de-Port. The labial and lingual borders are nearly parallel: the labial side is somewhat more convex than the lingual one. The cusps are perfectly aligned following the antero-posterior axis of the crown; they form a sharp cutting edge.

In anteriot view, the main cusp is perfectly straight and not curved towards the lingual side.

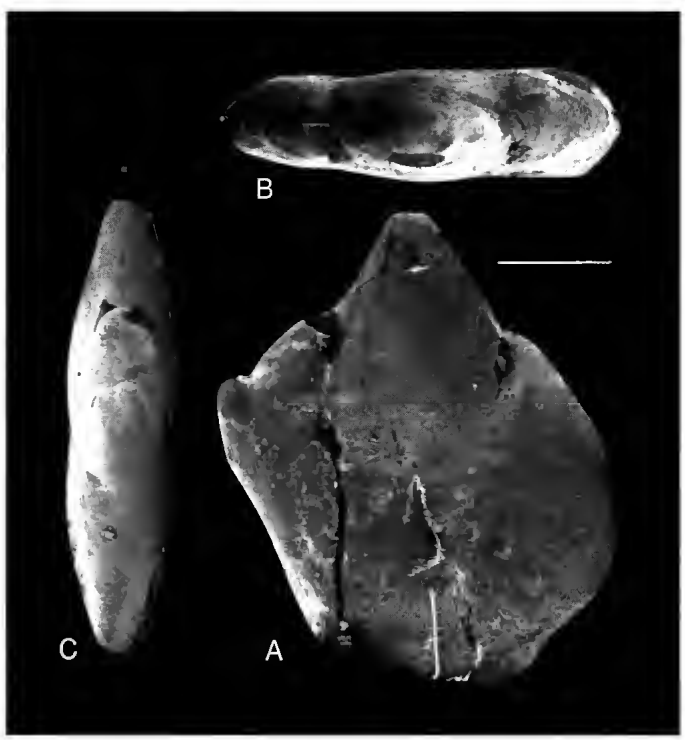

FIG. 17. — IRSNB R167, postcanine tooth of *Lepagia gaumensis*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, lateral view; **B**, occlusal view; **C**, ? anterior view. Scale bar: 1 mm.

TABLE 7. — Measurements (in mm) of the postcanine teeth of *Lepagia gaumensis*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown; **H**, height of the root. For the signification of the types, see text.

Group	Number	Lc	Wc	Hc	Hr	Lc/Wc	Hr/Hc
? II	IRSNB 28114/051	1.25	0.5	? 0.95	1	2.5	1.05
IV	IRSNB R167	3.65	1.05	2.7	1.7	3.47	0.63
	IRSNB 28114/104	2.65	0.85	1.8	-	3.12	-

In lateral view, the crown is more irregular, less symmetrical than in *Pseudotriconodon* or *Gaumia*. The main cusp, triangular in shape, is proportionally less high and its apex is less sharp than in the latter genera. It is flanked by one or two anterior, and by one or two posterior accessory cusps. In IRSNB 28114/104 and IRSNB R167, which possess two pairs of accessory cusps, the anterior accessory cusps are set higher on the edge of the main cusp than the posterior accessory cusps. The first pair of accessory cusps (median accessory cusps) is rather large, but not very sharp; on the other hand, the second pair (lateral accessory cusps) is smaller, but sharper. The crown of IRSNB 28114/051 is very eroded. Its main cusp seems slightly inclined backwards; the anterior accessory cusp is small but very sharp, whereas the posterior one appears as a vague ondulation of the posterior edge of the main cusp.

As in *Pseudotriconodon* and *Gaumia*, wear is erratic on the apex of the cusps and does not form clearly defined facets. There is no trace of cingulum. The crown and the root are separated by a well marked constriction.

Root

The root is undivided and never clearly higher than the crown: the ratio "height of the root/height of the crown" is about 1.05 in IRSNB 28114/051 and 0.63 in IRSNB R167. In anterior view, it is always very narrow. In lateral view, the root of IRSNB R167 has an irregular trapezoidal outline. Its length is greater than its height. Its anterior border is straight and oblique backwards and its posterior border is clearly convex. The root of IRSNB 28114/051 is proportionally higher; its anterior and posterior borders are slightly convex and nearly parallel.

The tip of the root is well preserved in IRSNB R167. It is long and nearly straight. The pulpal foramen is restricted to a long, very narrow and undivided slit.

DISCUSSION

IRSNB 28114/051 and IRSNB R167 are similar to the postcanine teeth of *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987 from the Rhaetian of Habay-la-Vieille (Belgian Lorraine) and Hallau (Switzerland): the crown is asymmetrical and irregular, there is a well marked constriction

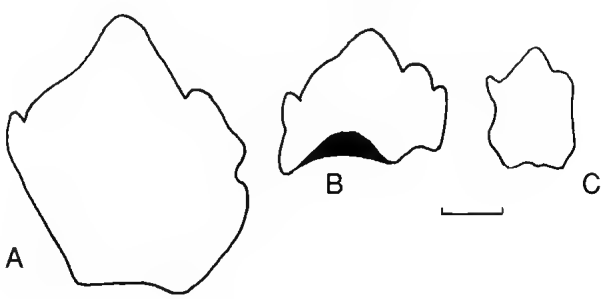

FIG. 18. — Outline of postcanine teeth of *Lepagia gaumensis*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, IRSNB R167; **B**, IRSNB 28114/104; **C**, IRSNB 28114/51. Scale bar: 1 mm.

between the crown and the root, the root is proportionally low and subtrapezoidal, the pulpal canal is a long and narrow slit.

The identification of IRSNB 28114/104 is more problematical because of its broken root. The shape of the crown resembles that of *Lepagia gaumensis*, but erratic enamel ridges can be observed on the labial side of the apex of the main cusp. Nevertheless, this character is too poorly expressed to justify the creation of a new species. Waiting for further evidence, this tooth is tentatively identified as *Lepagia gaumensis*.

Hahn *et al.* (1987) compare the mandible of *Lepagia gaumensis* with that of *Probainognathus*: in both taxa, the splenial is very narrow and extends halfway up on the lingual side of the dentary. As a result of this comparison, *Lepagia* is grouped within the family Chiniquodontidae. Battail (1989) observed a comparable reduction of the splenial in all the other families of advanced cynodonts, correlatively to the development of the dentary. Moreover, the horizontal ramus of the mandibule is much lower in *Lepagia* than in the Chiniquodontidae and is rather reminiscent of the mandible of the Dromatheriidae. Nevertheless, the root of the postcanine teeth is not subdivided in *Lepagia*, as in the Dromatheriidae. Thus, in the current state of our knowledge, it is not possible to state precisely the systematic position of *Lepagia gaumensis* within the Cynodontia.

TABLE 8. — Measurements (in mm) of the cynodont premolariform teeth, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown. For the signification of the forms, see text.

Form	Number	Lc	Wc	Hc	Lc/Wc	Lc/Hc
1	IRSNB 28114/029	1.4	0.65	-	2.15	-
	IRSNB 28114/032	1.45	0.58	1.9	2.5	0.76
	IRSNB 28114/039	1.13	0.68	1.43	1.66	0.79
	IRSNB 28114/114	1.25	0.55	-	2.27	-
	IRSNB 28114/116	1.4	0.65	-	2.15	-
	IRSNB 28114/118	1.05	0.6	1.2	1.75	0.87
	IRSNB 28114/119	1.25	0.7	1.47	1.79	0.85
	IRSNB 28114/120	1.65	0.88	2.3	1.87	0.71
	IRSNB R168	2.4	1.2	3.95	2	0.61
	IRSNB 28114/755	1.9	0.85	-	2.24	-
	IRSNB 28114/765	1.87	1	2.48	1.87	0.75
	IRSNB 28114/904	2.15	1.25	2.82	1.72	0.76
	IRSNB 28114/911	1.12	0.57	>1.58	1.96	> 0.7
	IRSNB 28114/973	1.5	0.98	1.83	1.53	0.82
	IRSNB 28114/000	2.13	1.25	?	1.7	?
	IRSNB 18114/925	1.68	1	?	1.68	?
	MNHP SNP83DD	2.37	1.15	3.27	2.06	0.72
	MNHP SNP58W	1.52	0.7	-	2.17	-
	MNHP SNP136W	0.95	0.53	1.05	1.79	0.9
	MNHP SNP159W	1.32	0.5	1.5	2.64	0.88
	MNHP SNP214W	1.73	0.98	-	1.76	-
	MNHP SNP215W	1.28	0.64	1.57	2	0.82
	MNHP SNP282W	0.73	0.35	1.05	2.09	0.7
	MNHP SNP328W	0.7	0.32	0.77	2.18	0.91
	MNHP SNP342W	0.88	0.48	-	1.83	-
	MNHP SNP395W	2.04	1.1	3.11	1.85	0.66
	MNHP SNP402W	2.21	-	3.24	-	0.68
	MNHP SNP404W	1.57	0.77	-	2.04	-
	MNHP SNP443W	0.58	0.33	0.68	1.76	0.85
	MNHP SNP451W	1.3	0.51	-	2.55	-
	MNHP SNP468W	2.15	1.16	3.28	1.85	0.66
2	IRSNB R169	1.5	0.65	-	2.3	-
	MNHP SNP95L	1.07	0.35	-	3.05	-
	MNHP SNP12W	2.19	1.19	-	1.84	-
	MNHP SNP85W	1.39	0.68	1.49	2.04	0.93
3	IRSNB R170	2.15	1	3.8	2.15	0.57
4	IRSNB R171	2.25	1.05	1.9	2.14	1.18
5	IRSNB 28114/877	0.75	0.18	-	4.17	-
6	MNHP SNP484W	1.8	0.47	1.42	3.83	1.27

Premolariform teeth incertae sedis

Teeth with a slender crown composed by a high anterior cusp and by a small posterior accessory cusp are described and discussed in the present chapter. Biometrical data observed on these teeth are shown in table 8. Six categories can be distinguished, on the basis of the general morpho-logy of their crown.

Form I
(Figs 19A, B, 20)

Material examined. — Specimens discovered in Saint-Nicolas-de-Port: IRSNB R168, IRSNB 28114/000, IRSNB 28114/029, IRSNB 28114/032, IRSNB 28114/039, IRSNB 28114/114, IRSNB 28114/116, IRSNB 28114/118, IRSNB 28114/119, IRSNB 28114/120, IRSNB 28114/755, IRSNB 28114/765, IRSNB 28114/904, IRSNB 28114/911,

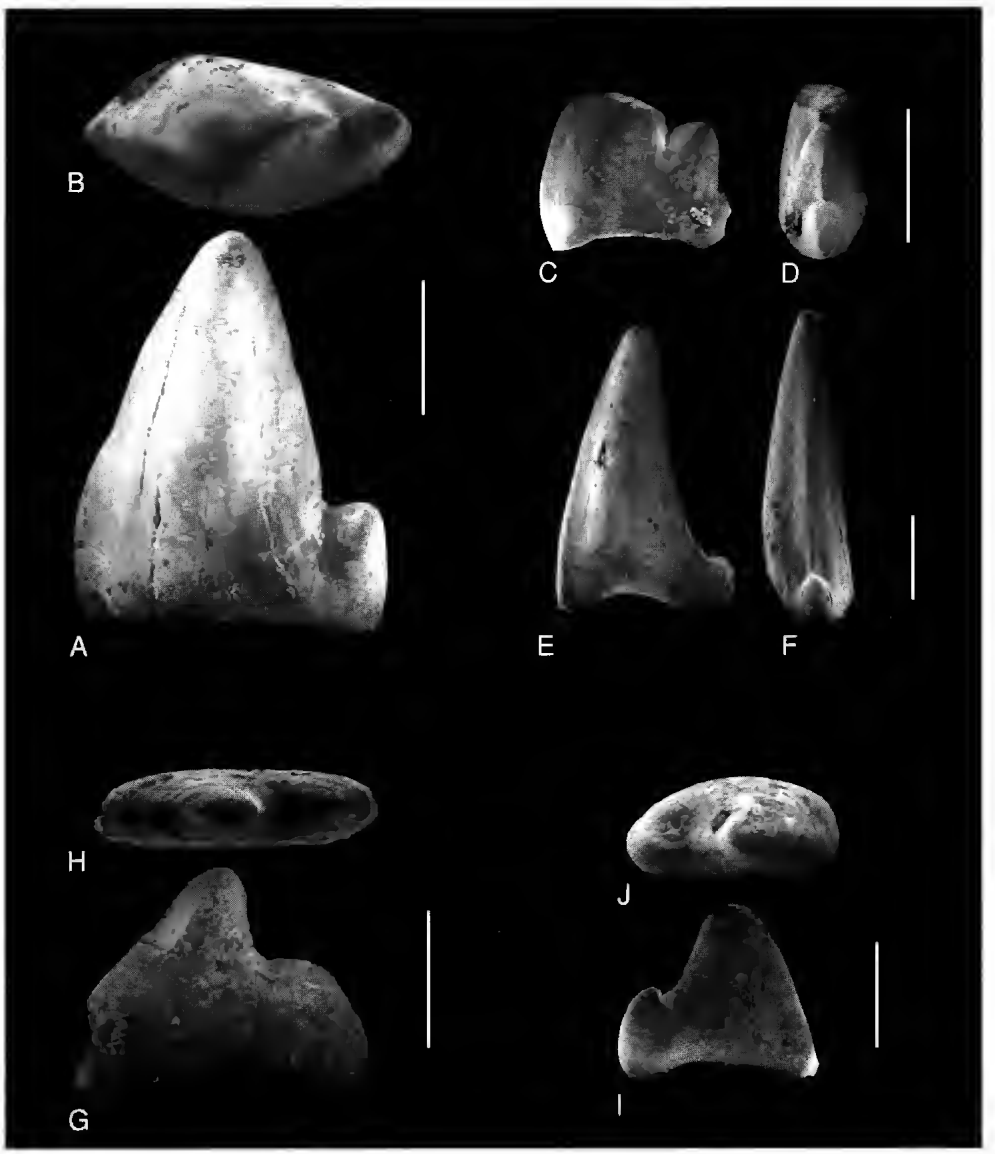

Fig. 19. — Cynodont premolariform teeth, from the Late Triassic of Saint-Nicolas-de-Port. **A**, **B**, IRSNB R168, form 1; **C**, **D**, IRSNB R169, form 2; **E**, **F**, IRSNB R170, form 3; **G**, **H**, MNHP SNP484W, form 6; **I**, **J**, IRSNB R171, form 4. A, C, E, G, I, lateral views; B, H, J, apical views; D, F, posterior views. Scale bars: 1 mm.

IRSNB 28114/925, IRSNB 28114/973, MNHP SNP72DD, MNHP SNP83DD, MNHP SNP58W, MNHP SNP136W, MNHP SNP159W, MNHP SNP214W, MNHP SNP215W, MNHP SNP282W, MNHP SNP328W, MNHP SNP342W, MNHP SNP395W, MNHP SNP402W, MNHP SNP404W, MNHP SNP443W, MNHP SNP451W, MNHP SNP468W.

Description

Premolariform teeth of form 1 are, by far, the most numerous. The crown is rather slender (0.61 < ratio "length/height" of the crown < 0.93), but their base is relatively robust (1.53 < ratio "length/width" of the crown < 2.55).

The main cusp is high and has a triangular outline in lateral view. It is curved backwards and slightly towards the lingual side. Its apex is rather sharp on the highest crowns, but more rounded on the smallest teeth. Nevertheless, it must be noted that the apex of the cusp can be partially eroded. Its anterior border is very convex: its base is usually thinner than its apical portion which can form a flatten edge. Its posterior edge is less convex, but very sharp along its whole height. Its labial side is convex anterio-posteriorly. Its lingual side forms a central convex ridge, flanked by an anterior and a posterior concave third. The posterior concavity is usually better marked than the anterior one.

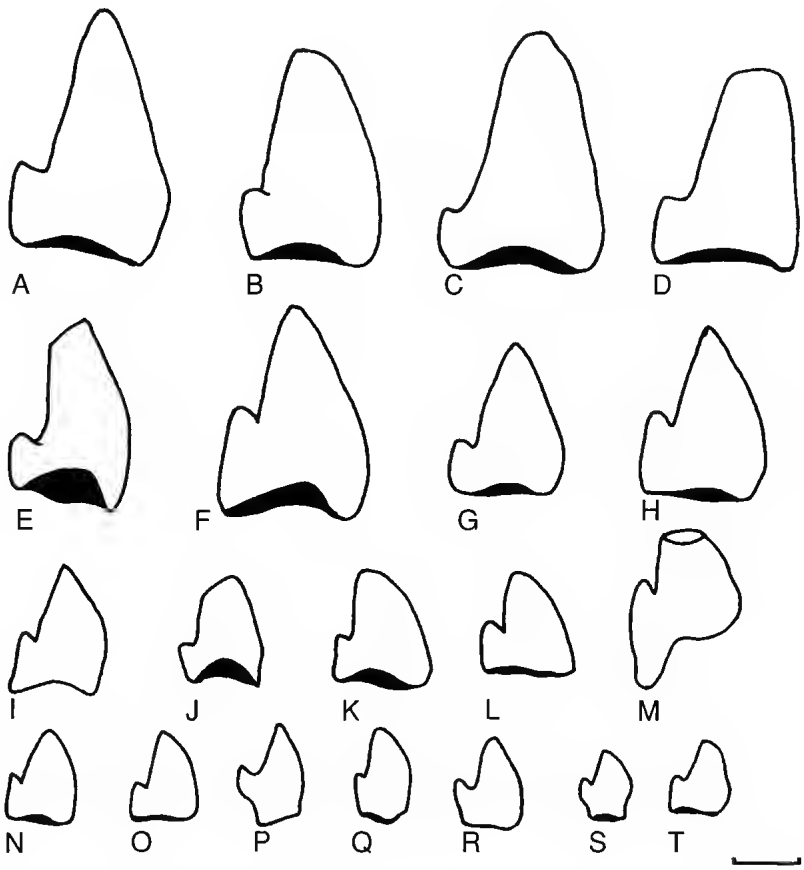

Fig. 20. — Outline of cynodont premolariform teeth (form 1), from the Late Triassic of Saint-Nicolas-de-Port. **A**, IRSNB R168; **B**, MNHP SNP395W; **C**, MNHP SNP468W; **D**, MNHP SNP492W; **E**, MNHP SNP58W; **F**, MNHP SNP83DD; **G**, IRSNB 28114/765; **H**, IRSNB 28114/904; **I**, IRSNB 28114/32; **J**, IRSNB 28114/29; **K**, IRSNB 28114/973; **L**, IRSNB 28114/648; **M**, MNHP SNP214W; **N**, IRSNB 28114/39; **O**, IRSNB 28114/119; **P**, MNHP SNP342W; **Q**, MNHP SNP382W; **R**, MNHP SNP136W; **S**, MNHP SNP443W; **T**, MNHP SNP78. Scale bar: 1 mm.

The posterior accessory cusp is always very reduced and triangular in lateral view. Its maximum height can reach the third of the height of the main cusp. Its apex is not very sharp. Its vertical axis usually slopes backwards.

Wear can affect the apex of the cusps, but does not form clearly defined facets. The crown is distinctly separated from the root by a constriction, particularly well marked on the anterior and the posterior sides of the teeth (MNHP SNP342W, MNHP SNP443W, MNHP SNP451W). The root is not preserved in the premolariform teeth discovered in Saint-Nicolas-de-Port.

DISCUSSION

Premolariform teeth of form 1 appear, at first sight, morphometrically heterogeneous: the small crowns seem proportionally much lower than the taller ones. Figure 22 shows the relative growth of the length (in Ln) and the height (in Ln) of the crown in the premolariform teeth discovered in Saint-Nicolas-de-Port. The coefficient of correlation calculated for the teeth of form 1 is astonishingly high: r = 0.985. The allometry coefficient b, calculated according to Teissier's (1948) formula, is 1.21. The apparent morphometrical heterogeneity of these teeth can therefore be easily explained by the positive allometry between the length and the height of the crown: the height grows more quickly than the length. Figure 23 shows that the length and the width of the crown, in the premolariform teeth of form 1, can be regarded as isometrical: b = 1.05; r = 0.94. In conclusion, it can be assumed that the morphometrical variability observed in these teeth reflects ontogenetical differences and/or the position in the jaw, instead of taxonomic heterogeneity.

Form 2
(Figs 19C, D, 21A-C)

MATERIAL EXAMINED. — Specimens discovered in Saint-Nicolas-de-Port: IRSNB R169, MNHP SNP 95L, MNHP SNP12W, MNHP SNP85W.

DESCRIPTION

The premolariform teeth grouped in form 2 differ from the other forms by a second small accessory cusp, posteriorly. It is very reduced and reaches only the quarter of the height of the first accessory cusp. The proportions of the crown are similar to those observed in the premolariform teeth of form 1 (see Table 8, Figs 22, 23). The asymmetry between the lingual and the labial sides of the main cusp is less marked than in the premolariform teeth of form 1. In anterior view, the main cusp is slightly curved towards the lingual side of the tooth. Hahn *et al.* (1994) describe a well defined wear facet on the labial side of MNHP SNP12W: this is therefore a lower premolariform tooth. The base of the anterior

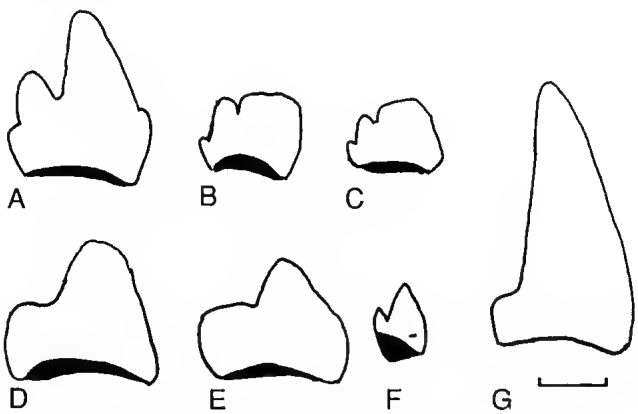

FIG. 21. — Outline of cynodont premolariform teeth, from the Late Triassic of Saint-Nicolas-de-Port. **A**, MNHP SNP85W (form 2); **B**, IRSNB R169 (form 2); **C**, MNHP SNP95L (form 2); **D**, IRSNB R1471 (form 4); **E**, MNHP SNP484W (form 6); **F**, IRSNB 28114/877 (form 5); **G**, IRSNB R170 (form 3). Scale bar: 1 mm.

border of the main cusp is very sharp in IRSNB R169. In MNHP SNP85W, a small swelling on the base of the anterior edge of the main cusp can tentatively be interpreted as the rough shape of an anterior accessory cusp. The base of the crown is clearly separated from the root by a constriction, as in the premolariform teeth of form 1. The root is not preserved in the known material.

DISCUSSION

Hahn *et al.* (1994) refer SNP 12W to *Tricuspes sigogneauae*. This identification is mainly based on the position of the second accessory cusp, on the posterior wall of the crown. Nevertheless it seems that, in the present case, this character mainly reflects the low development of this cusp. Thus, because of the important diversity of the cynodont fauna from Saint-Nicolas-de-Port, this identification is doubtful, in the absence of jaw fragments associating both premolariform and molariform teeth (see below).

The morphological differences observed between the premolariform teeth of form 1 and form 2 can perhaps be interpreted as differences of position in the tooth row: premolariform teeth of form 1 should be set in a more anterior position than premolariform teeth of form 2.

Form 3
(Figs 19E, F, 21G)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R170.

DESCRIPTION

IRSNB R170 is characterized by its very high, slender and caniniform crown: the ratio "length/height" of the crown is 0.57 (see Fig. 22). On the other hand, the ratio "length/width" of the crown, which is 2.15, has a usual value, as in the premolariform teeth of form 1 or 2. Both the labial and the lingual sides of the main cusp are nearly symmetrically convex. The main cusp has, in lateral view, a triangular outline and is curved backwards. Its apex is slightly blunt. Its posterior edge is very sharp. Its anterior border forms a flattened edge, on its whole height. Along the anterior border of its lingual side, it bears a long, elliptical and flatten wear facet. If the orientation proposed for this tooth is correct, it is thus an upper premolariform. The posterior accessory cusp is tiny: it is only represented by a small swelling at the base of the posterior border of the main cusp. The root is not preserved.

DISCUSSION

The very slender aspect of the crown (see

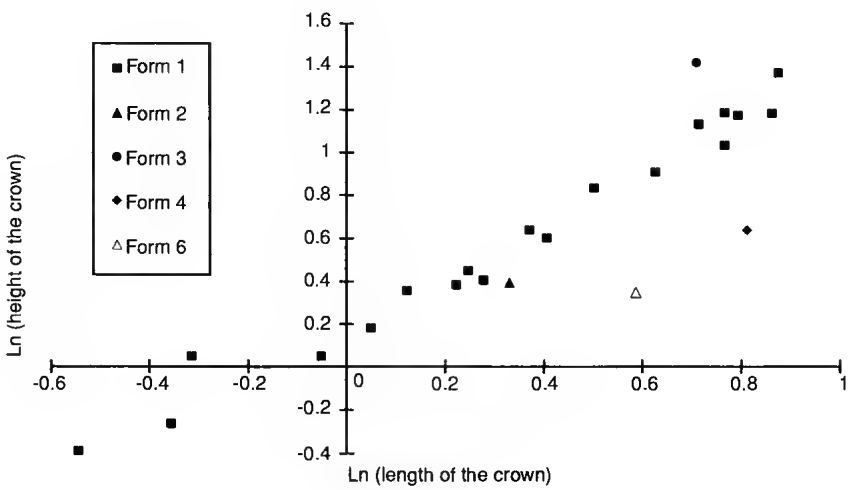

FIG. 22. — Dispersion diagram (length/height) of the cynodont premolariform teeth.

Fig. 22) and the tiny posterior accessory cusp distinguish IRSNB R170 from the other premolariform teeth discovered in Saint-Nicolas-de-Port. These differences could reflect a more anterior position of this specimen in the tooth row of the animal. Nevertheless the presence of a well marked wear facet, not observed in the premolariform teeth of forms 1 and 2, indicates that this tooth probably belongs to another taxon.

Form 4
(Figs 19I, J, 21D)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R171.

DESCRIPTION
Contrary to IRSNB R170, this tooth is very stocky: the ratio "length/height" of the crown is 1.18. The ratio "length/width" of the crown, which is 1.14, is usual, as in the other forms of premolariform teeth previously described. The labial and lingual sides of the crown are quite asymmetrical: the labial side is very convex antero-posteriorly and the lingual one, straight. The main cusp is low, stocky and triangular in outline. Its apex is rounded and bears a small elliptical wear facet, showing the dentine, on its labial side. If the orientation proposed for this tooth is correct, IRSNB R171 is thus a lower premolariform. Both the anterior and posterior edges of the main cusp are not very sharp. The posterior accessory cusp, weakly developed and very rounded, reaches the quarter of the height of the main cusp. At the junction between the two cusps, the labial side of the crown bears a small dimple. The root is not preserved.

DISCUSSION
Figure 22 shows that this tooth is morphometrically different from the other premolariform teeth discovered in Saint-Nicolas-de-Port (except MNHP SNP484W) because of its low and stocky crown. The very rounded apex of the cusps is an unusual feature, too.

Form 5
(Fig. 21F)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB 28114/877.

DESCRIPTION
This fragmentary dental crown is very small and extremely thin: the ratio "length/width" of the crown is 4.17. The main cusp has, in lateral

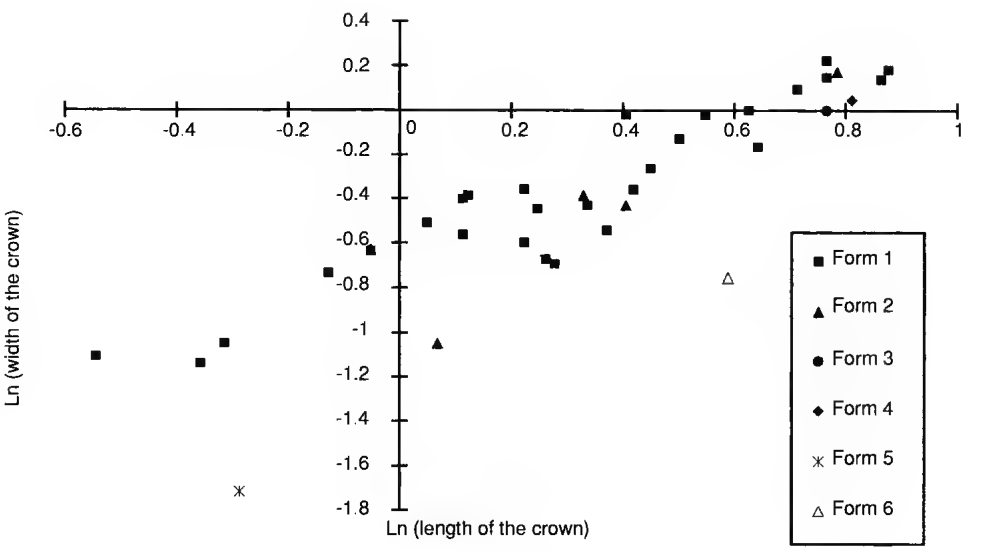

FIG. 23. — Dispersion diagram (length/width) of the cynodont premolariform teeth.

view, a triangular outline and is rather elongated antero-posteriorly. Its apex is very sharp and both its anterior and posterior edges are extremely sharp, too. The anterior edge is slightly longer than the posterior one and, therefore, the main cusp slopes slightly backwards. The posterior accessory cusp is triangular and very sharp, too. It reaches the half of the height of the main cusp. The base of the crown is broken, but seems particularly high.

DISCUSSION
IRSNB 28114/877 differs from the other premolariform teeth discovered in Saint-Nicolas-de-Port because of its extremely narrow crown (see Fig. 23) and its very sharp edges.

Form 6
(Figs 19G, H, 21E)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: MNHP SNP484W

DESCRIPTION
MNHP SNP484W is characterized by its proportionally long, low and narrow crown: the ratio "length/width" of the crown is 3.83 and the ratio "length/height" of the crown, 1.27. Both the labial and the lingual sides of the crown are symmetrically antero-posteriorly convex. The edge is sharp on the whole length of the crown. The main cusp is short, not very high and triangular in outline. Both its anterior and posterior cutting edges are slightly convex. Its apex is rather rounded. The posterior accessory cusp is quite low and rounded, but very elongated antero-posteriorly. At the base of the anterior edge of the crown, an elliptical flattened surface, showing the dentine, probably represents a contact facet with the anterior adjacent crown in the tooth row. The base of the crown seems constricted.

DISCUSSION
MNHP SNP484W is clearly different from the other premolariform teeth discovered in Saint-Nicolas-de-Port: the proportions of the crowns are unusual (see Figs 22, 23), the main cusp is very short and low, the accessory cusp is proportionally very long and the contact area, at the base of the crown, is not present in the other specimens. Consequently, it probably belongs to another taxon.

AFFINITIES OF PREMOLARIFORM TEETH FROM SAINT-NICOLAS-DE-PORT
Premolariform teeth similar to those discovered in Saint-Nicolas-de-Port have been described in primitive pterosaurs, Triassic cynodonts and early mammals.

Pterosaurs
Teeth similar to premolariforms discovered in Saint-Nicolas-de-Port are described in the pterosaur *Eudimorphodon ranzii* (Wild 1978). These are formed by a main cusp slightly curved backwards, with a sharp-pointed apex and a very sharp edge, and by a small posterior accessory cusp. Nevertheless, the enamel bears numerous longitudinal ridges and the crown is less compressed labio-lingually. "Premolariform" teeth of *Eudimorphodon* are preserved in the Upper Triassic of Saint-Nicolas-de-Port, too (Godefroit & Cuny, in prep.).

Cynodonts
The general pattern of premolariform teeth discovered in Saint-Nicolas-de-Port can be observed in several groups of Triassic cynodonts.
Thrinaxodontidae. In *Thrinaxodon liorhinus* Seeley, 1895, from the Early Triassic of South Africa, the most anterior upper postcanines are compressed labio-lingually and bicuspid, with an anterior main cusp and a posterior accessory cusp. Nevertheless, these always bear a well developed lingual cingulum (Battail 1991).
Galesauridae. In *Galesaurus* Owen, 1860, from the Early Triassic of South Africa, both the upper and the lower postcanines are compressed labio-lingually, bicuspid, without distinct anterior accessory cusp and without cusped cingulum (Battail 1991). Nevertheless, they differ from the premolariform teeth from Saint-Nicolas-de-Port in their main cusps very curved backwards and in their posterior accessory cusp proportionally higher.
Cynognathidae. In *Cynognathus crateronotus*

Seeley, 1895, from the Early Triassic and Early Middle Triassic of South Africa, the postcanine teeth are always compressed labio-lingually, very sharp and devoid of cingulum. In the largest specimens, the most anterior postcanines are very similar to the premolariform teeth from Saint-Nicolas-de-Port, with a high main cusp slightly curved backwards and a small posterior accessory cusp. Nevertheless these teeth are clearly larger in *Cynognathus*. The juvenile specimens have a more complex postcanine structure (Battail 1991).

Chiniquodontidae. Sectorial and bicuspid postcanine teeth can be observed in *Probelesodon lewisi* Romer, 1969 and *Probainognathus jenseni* Romer, 1970, from the Middle Triassic of Argentina. In *Probainognathus*, the main cusp is very low and not very developed and, moreover, the edge of the crown is sinuous, without well defined accessory cusp. The postcanine teeth of *Probelesodon* are typically bicuspid: only the most posterior postcanines possess an anterior accessory cusp. Nevertheless, the main cusp is always more curved backwards than in the premolariform teeth from Saint-Nicolas-de-Port.

Tritheledontidae. If bicuspid dental crowns are present in *Pachygelenus monus* Watson, 1913, *Tritheledon riconoi* Broom, 1912 and *Diarthrognathus broomi* Crompton, 1958, from the Late Triassic of South Africa, these teeth are never as strictly sectorial as in the premolariform teeth from Saint-Nicolas-de-Port.

Dromatheriidae. The postcanine teeth of the Dromatheriidae are always strictly sectorial, without developed cingulum and with a cutting edge. In *Dromatherium sylvestre* Emmons, 1857, from the Late Triassic of the United States, some postcanines seem typically bicuspid: the posterior accessory cusp is either smaller than the main cusp or almost of the same size. The root is always double and, contrary to the premolariform teeth discovered in Saint-Nicolas-de-Port (at least in the forms 1, 2 and 6), there is no constriction between the crown and the root. It is interesting to observe that, in *Dromatherium*, these "premolariform" teeth are set more posteriorly than the tricuspid teeth. Premolariforms are not recorded in other species, only known by very fragmentary material or by isolated teeth. As explained above, the premolariform teeth attributed to *Tricuspes sigogneauae* by Hahn *et al.* (1994) are here more cautiously referred to Cynodontia indet.

Early mammals

Morganucodontidae. (Rhaetian and Early Liassic of Western Europe, Groenland, China and South Africa). Morganucodontidae are represented in Saint-Nicolas-de-Port by isolated molars of *Brachyzostrodon coupatezi* Sigogneau-Russell, 1983 and *Brachyzostrodon maior* Hahn, Sigogneau-Russell *et* Godefroit, 1991. Other taxa are also present but have not been described yet. In the Morganucodontidae, the premolariform teeth present a similar structure as those discovered in Saint-Nicolas-de-Port.

In *Morganucodon* Kühne, 1949 the premolars are formed by two cusps, as in the premolariforms discovered in Saint-Nicolas-de-Port. Nevertheless, the crown is less narrow labio-lingually and the anterior side is rounded and sometimes even bulbous. The main cusp is more elongated antero-posteriorly. A weak cingulum seems always present. The root is double (Mills 1971; Kermack *et al.* 1973; pers. obs.).

In *Megazostrodon rudnerae* Crompton *et* Jenkins, 1968, pm2 and PM4 are bicuspid and they seem devoid of cingulum. Nevertheless, they clearly differ from premolariform teeth discovered in Saint-Nicolas-de-Port by their more stocky and bulbous appearance (see Crompton 1974, figs 4-6).

In *Erythrotherium parringtoni* Crompton, 1964, pm2 and pm3 resemble the premolariform teeth from Saint-Nicolas-de-Port in being bicuspid and apparently devoid of cingulum. Nevertheless, as in the other Morganucodontidae, these teeth look less secrorial and more bulbous.

Kuehneotheriidae. (Rhaetian and Early liassic of Western Europe, Groenland and India). Theria are represented, in Saint-Nicolas-de-Port, by the Woutersiidae *Woutersia* Sigogneau-Russell, 1983 and by other undescribed Kuehneotheriidae. Premolars are known in the Kuehneotheriidae *Kuehneotherium praecursoris* Kermack, Kermack *et* Mussett, 1968. They differ from the premolariform teeth discovered in

Saint-Nicolas-de-Port by their more elongated and more curved main cusp and also by the frequent presence of a small anterior accessory cusp and of cingular elements.

CONCLUSIONS

From the preceding comparisons, it appears that the premolariform teeth discovered in Saint-Nicolas-de-Port have evident affinities with the cynodonts. In the other groups of reptiles, only the pterosaur *Eudimorphodon* has dental crowns with a similar structure, but with numerous and well marked enamel ridges. In the early mammals Morganucodontidae and Kuehneotheriidae, the crowns of the premolars are more bulbous and usually possess cingular elements.

The premolariform teeth from Saint-Nicolas-de-Port do not show clear diagnostical characters allowing their strict identification at the family level. The attribution of several premolariform teeth to the species *Tricuspes sigogneauae*, proposed by Hahn *et al.* (1994), is here regarded as doubtful. The absence of preserved root is particularly determinant. The morphological and morphometrical variability of the crown permits the distinction of six "forms". This heterogeneity probably reflects the presence of several taxa in this material. If dromatheriids had alternating (and continuous) replacements like in *Therioherpeton*, it can not be excluded that premolariform teeth represent, in fact, replaced deciduous teeth, which must be numerous in the fossil sample.

GOMPHODONT CYNODONTS

Family TRAVERSODONTIDAE von Huene, 1936

PRELIMINARY REMARKS

Hopson (1984, 1985) thinks that the Traversodontidae represent a paraphyletic group: he believes that the ancestry of the family Tritylodontidae lies within it. Therefore, the Traversodontidae are not strictly monophyletic, but rather represent a grade group. On the other hand, Battail (1991) recognizes the Traversodontidae as a monophyletic group: the Tritylodontidae should form the sister-group of the Traversodontidae.

It is interesting to note that the Traversodontidae, known by complete skull material, are relatively small forms in the late Early Triassic (*Pascualgnathus*, *Andescynodon*...), medium-sized forms in the early Middle Triassic (*Scalenodon*, *Massetognathus*...) and large to very large forms in the late Middle Triassic and in the early Late Triassic (*Exaeretodon*, *Ischignathus*, *Scalenodontoides*...). It is therefore rather surprising to find, in deposits dated from the very end of the Triassic, tiny teeth which, on the basis of their structure, seem to be attributable to traversodontids. It cannot be excluded, however, that the taxonomic position of these forms might be reevaluated, should more complete material reveal major anatomical differences with the typical, well known Traversodontidae.

Genus *Maubeugia* n.g.

TYPE SPECIES. — *Maubeugia lotharingica* n.sp.

DERIVATIO NOMINIS. — Dedicaced to Dr. P.-L. Maubeuge, for his contribution to the knowledge of the geology and palaeontology of the Lorraine area and for his active participation in the exploration of the quarry of Saint-Nicolas-de-Port.

DIAGNOSIS. — As for the only currently recognized species *Maubeugia lotharingica* n.sp.

DISCUSSION

See below.

Maubeugia lotharingica n.sp.
(Figs 24, 25)

HOLOTYPE. — IRSNB R172, a left upper postcanine, with its root nearly completely preserved.

DERIVATIO NOMINIS. — *lotharingicus*, *-a*, *-um* (lat.) = from Lorraine (north-eastern France).

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

STRATUM TYPICUM. — "Rhaetian" sandstones. Upper Triassic.

DIAGNOSIS. — Traversodontidae known by only one upper postcanine tooth, with the following characters: crown very small (width = 0.80 mm) with an ovoid

outline in occlusal view (ratio "length/width" of the crown = 0.80); labial side longer, but less convex than the lingual side. Main labial cusp somewhat higher than the lingual one. Transverse ridge set behind the middle of the crown, but not merged with the posterior cingulum; anterior basin consequently larger than the posterior basin. Well developed central cusp on the transverse ridge, close to the labial main cusp and separated from the lingual cusp by an embayment. Large antero-labial accessory cusp connected to the main labial cusp by a prominent ridge. Both anterior and posterior "cingula" very low and very poorly expressed.

Description

Orientation

The orientation of IRSNB R172 proposed here is mainly based on comparisons with the upper postcanines of *Scalenodon charigi* Crompton, 1972 and *Boreogomphodon jeffersoni* Sues *et* Olsen, 1990, which closely resemble this tooth. In the Traversodontidae, the upper postcanines are clearly wider (labio-lingually) than long (mesio-distally). As in advanced Traversodontidae, the transverse ridge of IRSNB R172 is set behind the middle of the tooth and the anterior basin is therefore better developed than the posterior one. The buccal side is longer and less convex than the lingual side. A tall accessory cusp is set on the antero-labial margin of the crown. Thus, IRSNB R172 is a left upper postcanine.

Measurements

Length of the crown (= maximum mesio-distal diameter) = 0.65 mm; width of the crown (= maximum labio-lingual diameter) = 0.80 mm.

Crown

In occlusal view, the crown is subovoid in outline, wider than long (the ratio "length/width" of the crown = 0.81). The labial border is longer, but less convex than the lingual one; the anterior border is more convex than the posterior one. Three cusps are arranged to form a transverse row. The lingual cusp seems the widest and the central cusp is by far the smallest. The central cusp is closer to the labial cusp. The three main cusps are connected together by a transverse ridge. This ridge is set in a posterior position, behind the middle of the crown. A very large accessory cusp, nearly as wide as the labial cusp, is set on the antero-labial margin of the crown. The edges of both the main and the accessory labial cusps form a continuous ridge, parallel to the labial side of the crown. Very low ridges, respectively parallel to the anterior and the posterior margins of the crown, connect, on one hand, the accessory labial to the lingual cusps and, on the other hand, the main labial to the lingual cusps. A wide anterior basin is surrounded by the lingual side of the accessory labial cusp, by the antero-lingual side of the main labial cusp, by the anterior side of the central cusp and by the antero-labial side of the lingual cusp. A smaller and less well defined posterior basin occupies a corresponding position behind the transverse ridge: it is surrounded by the postero-lingual side of the main labial cusp, by the posterior side of the central cusp and by the postero-labial side of the lingual cusp.

In labial view, the main and the accessory labial cusps are separated from each other by a shallow indentation. The accessory cusp is somewhat lower than the main one. Their apices are very rounded. At the level of their junction, the anterior side of the crown forms a very small basin. The crown is separated from the root by a well marked constriction.

In lingual view, the lingual cusp seems lower than the main labial cusp, and its apex seems less rounded. At the base of the crown, a small, elliptical and deep depression can be observed. This is probably due to post-mortem distortion of the specimen.

In anterior view, the crown has a bell-mouthed outline. Both labial and lingual sides are convex dorso-ventrally; the lingual wall is somewhat more convex than the labial one. The main labial cusp is the highest. It is connected to the central cusp by a prominent ridge with anterior wall nearly vertical. The central cusp is separated from the lingual cusp by a rather deep indentation. The transverse ridge passes on the labial side of the lingual cusp. The crest connecting the accessory labial cusp to the lingual cusp ("anterior cingulum") is quite low and forms tiny undulations. The constriction between the crown and the root is very clearly marked.

In posterior view, the posterior wall of the portion of the transverse ridge connecting the labial

and the central cusps is less vertical than the anterior wall. The ridge connecting the main labial and the lingual cusps ("posterior cingulum") is very low and not very developed.

Root

The tip of the root is broken. Complete, the root was probably much higher than the crown. In lingual view, it is subrectangular in shape: its anterior and posterior sides are straight and nearly parallel. In anterior view, the root is gently tapering to the tip. The posterior border is more oblique than the anterior one.

Discussion

The morphology of the upper postcanines is very variable in the Traversodontidae: therefore, they are very useful to establish the phylogenetical relationships of the different genera within this family (Battail 1989). Thus, it is interesting to compare IRSNB R172 with the upper postcanines in currently known traversodonts.

Pascualgnathus Bonaparte, 1966
Andescynodon Bonaparte, 1969
Rusconiodon Bonaparte, 1970
(Lower Triassic of Argentina)

The upper postcanines of these small and primitive Traversodontidae share several plesiomorphic characters (Battail 1989). Contrary to IRSNB R172, the transverse ridge connecting the labial and the lingual cusps is set anteriorly, in the anterior part of the crown. The posterior basin is consequently larger than the anterior one. There is no trace of central cusp. An accessory cusp is present, posteriorly to the main labial cusp. Both the anterior and the posterior cingula are well developed.

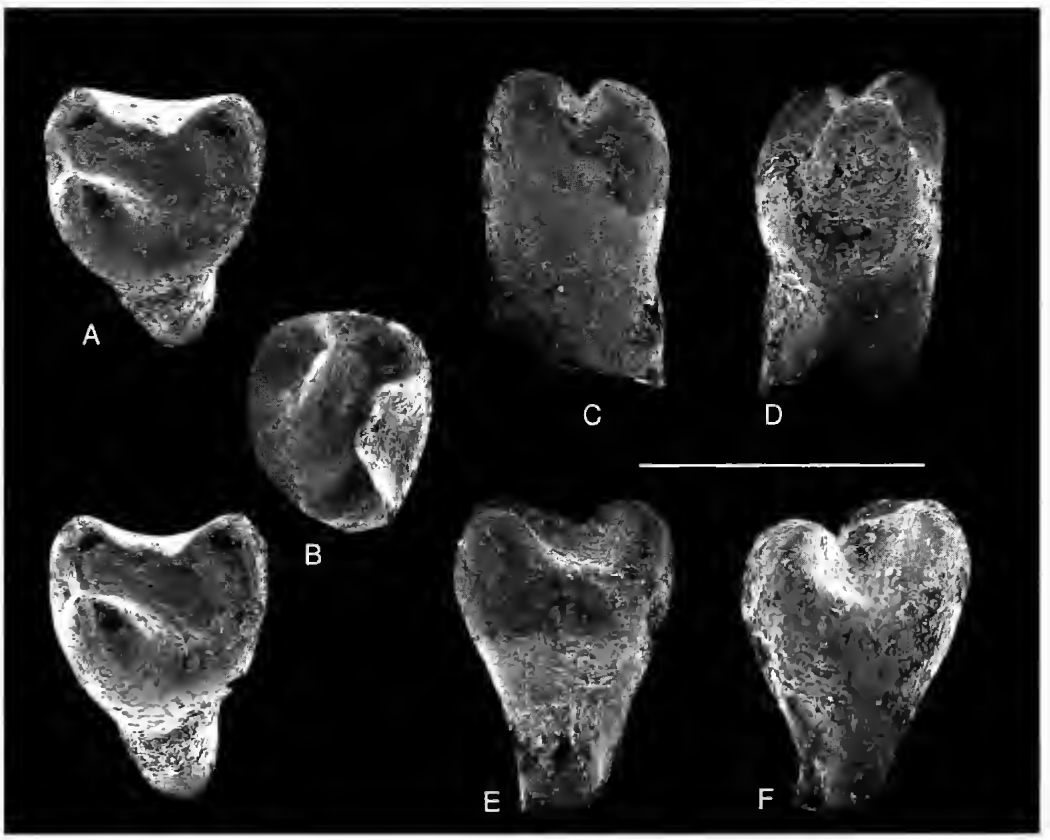

Fig. 24. — IRSNB R172, left upper postcanine of *Maubeugia lotharingica*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, stereophotographs; **B**, occlusal view; **C**, labial view; **D**, lingual view; **E**, anterior view; **F**, posterior view. Scale bar: 1 mm.

Scalenodon Crompton, 1955
(Middle Triassic of Tanzania, Zambia and ? Russia)
The different species in the genus *Scalenodon* (*sensu* Battail 1991) differ mainly from each other in the structure of their postcanine teeth. The differences observed in the Tanzanian species are summarized by Crompton (1972, table 1). The transverse ridge is always set posteriorly, behind the middle of the crown, like in IRSNB R172. The anterior basin is therefore much larger than the posterior basin. In several species, the transverse ridge, quite posteriorly set, merges with the posterior cingulum and the posterior basin is consequently lost. Except in *Scalenodon charigi* Crompton, 1972, the transverse ridge supports a well developed central cusp. The anterior and posterior cingula are more or less developed in the different species of *Scalenodon*. Antero-labial and/or antero-lingual accessory cusps are occasionally present. The upper postcanines of *Scalenodon* differ from IRSNB R172 in several details. The crown, much larger, is always proportionally wider. The labial side is usually more convex than the lingual one. The central cusp is set more lingually: it is connected to the lingual cusp by a prominent ridge and separated from the labial cusp by a deep embayment.

Massetognathus Romer, 1967
(Middle Triassic of Argentina)
In *Massetognathus*, the transverse ridge is set quite posteriorly and merges with the posterior cingulum; it supports a central cusp, close to the lingual cusp. The posterior basin is consequently

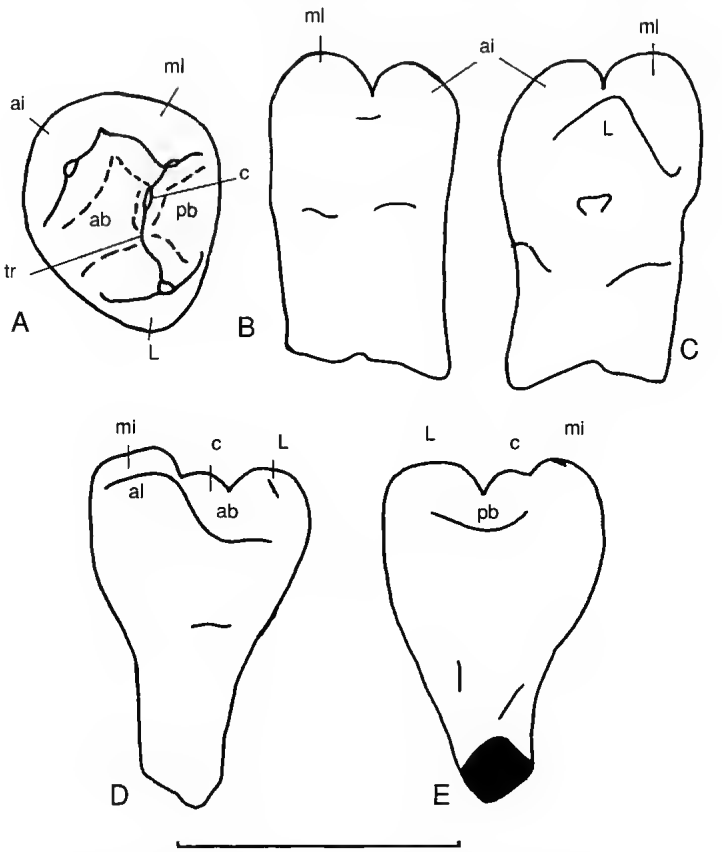

Fig. 25. — IRSNB R172, left upper postcanine of *Maubeugia lotharingica*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **ab**, anterior basin; **al**, antero-labial cusp; **c**, central cusp; **L**, lingual cusp; **ml**, main labial cusp; **pb**, posterior basin; **tr**, transverse ridge. Scale bar: 1 mm.

lost, but the anterior basin is enlarged. A large accessory cusp is set anteriorly and slightly lingually to the labial main cusp. The lingual wall of the crown looks therefore oblique. The labial side of the crown is very convex antero-posteriorly.

Traversodon von Huene, 1936
(Upper Triassic of Brazil)
In this latge Traversodontidae, the upper postcanines are proportionally much wider than in IRSNB 28114/113. The transverse ridge connecting the labial and the lingual cusps is set behind the middle of the crown and the anterior basin is somewhat larger than the posterior one. Contrary to IRSNB 28114/113, the lingual cusp is much higher than the labial one and there is neither central cusp nor accessory cusp.

Gomphodontosuchus von Huene, 1928
(Upper Triassic of Brazil)
In this genus, the transverse ridge connecting the lingual and the labial main cusps forms the posterior wall of the crown and is devoid of central cusp. A labial and a lingual accessoty cusps are set on the anterior margin of the crown and connected to the corresponding main cusp by a low ridge. The labial cusps are clearly set more anteriorly than the lingual ones. The anterior basin surrounded by these four cusps is particularly enlarged, but not very deep.

Exaeretodon Cabrera, 1943
(Upper Triassic of Argentina, Brazil and India)
Ischignathus Bonaparte, 1963
(Upper Triassic of Argentina)
The upper postcanines of these large Traversodontidae are formed by two main cusps connected by a low posterior transverse ridge, concave posteriorly and oblique. The main labial cusp is set much more anteriorly than the main lingual cusp. An accessory lingual cusp is set in front of the main lingual cusp. An accessory labial cusp forms an anterior lobe accommodated in the posterior concavity of the anterior adjacent tooth. Therefore, the crown of the upper postcanines has, in occlusal view, a characteristic geniculate outline. An accessory posterior cusp can occasionally be developed. The central cusp is apparently absent. The anterior basin is more or less enlarged in the different species.

Arctotraversodon Sues, Hopson *et* Shubin, 1992
(Upper Triassic of Canada)
The upper postcanines of this large Traversodontidae are very large and very compressed mesio-distally. The transverse ridge connecting the labial and the lingual cusps forms the posterior wall of the crown and supports a prominent central cusp. It is close to the lingual cusp and separated from the labial cusp by a deep embayment. There is no anterior accessory cusp. The anterior cingulum is well developed.

Microscalenodon Hahn, Lepage *et* Wouters, 1988
(Upper Triassic of Belgium)
The upper postcanines of *Microscalenodon* are, as IRSNB R172, very small. The crown is very compressed mesio-distally and its morphology is quite simple: a large lingual cusp and a small labial cusp are connected by a transverse ridge forming the posterior wall of the crown, without central cusp, accessory cusp and anterior cingulum.

Boreogomphodon Sues *et* Olsen, 1990
(Upper Triassic of the USA)
The upper postcanines of this genus closely resemble IRSNB R172. They are very small, less than 5 mm wide. The labial side is longer and less convex than the lingual one. The transverse ridge, set behind the middle of the crown, supports a well developed central cusp. A large antero-labial accessory cusp is connected to the main labial cusp by a prominent ridge. The anterior ridge ("anterior cingulum") connecting the accessory labial cusp to the lingual cusp is very low and poorly developed. Nevertheless, they differ in several details. The crown is proportionally wider in *Boreogomphodon*. The transverse ridge is set more posteriorly and the posterior basin is consequently lost. The central cusp is close to the lingual cusp and separated from the labial cusp by a deep embayment.

From these detailed comparisons with the upper postcanines in the different genera of Traversodontidae, it appears that IRSNB R172 shows an original set of morphological characters

justifying its attribution to a separate new genus:
– The crown is ovoid in occlusal view and not very compressed mesio-distally.
– The transverse ridge is set behind the middle of the crown, but does not participate in the posterior wall of the crown. The anterior basin is larger than the posterior basin.
– The transverse ridge supports a well developed central cusp, close to the labial cusp and separated from the lingual cusp by a deep embayment.
– The antero-labial accessory cusp is particularly well developed and connected to the main labial cusp by a prominent ridge.
– The tooth is very small.

In the structure of its upper postcanines, *Maubeugia* more closely resembles *Scalenodon* and *Boreogomphodon* than any other taxon. Figure 26 illustrates the possible phylogenetic relationships between the different genera of Traversodontidae. Although discovered in Late Triassic outcrops, *Maubeugia* looks, in the structure of its upper postcanines, rather "primitive". This cladogram, modified from Battail (1989, fig. 128), only reflects the modifications in the structure of the upper postcanines and is, therefore, very restrictive. A more definitive assessment of the phylogeny of the Traversodontidae must await an analysis of the whole skeleton in these gomphodont cynodonts.

Genus *Roseria* n.g.

TYPE SPECIES. — *Rosieria delsatei* n.sp.

DERIVATIO NOMINIS. — From the type locality Rosières-aux-Salines.

DIAGNOSIS. — As for the only currently recognized species *Rosieria delsatei* n.sp.

DISCUSSION
See under *Rosieria delsatei* n.sp.

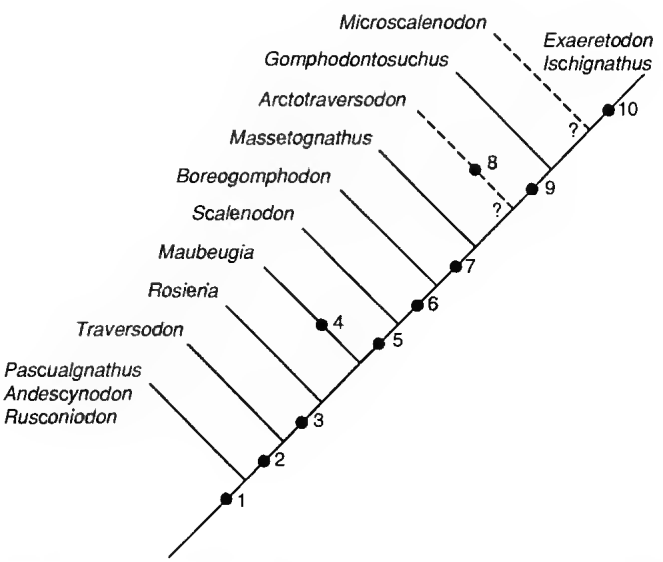

FIG. 26. — Possible phylogeny of the Traversodontidae, following the modifications of the structure of their upper postcanines (after Battail 1989, modified). **1**, upper postcanines mainly formed by one main lingual cusp and one main labial cusp, connected together by a transverse ridge; presence of cingula in front of and behind the transverse ridge; presence of one postero-labial accessory cusp. **2**, disparition of the postero-labial accessory cusp; transverse ridge set behind the middle of the crown. **3**, formation of a basin in front of the transverse ridge; apparition of one antero-labial accessory cusp. **4**, central cusp connected to the main labial cusp. **5**, central cusp connected to the lingual cusp. **6**, transverse ridge merging with the posterior cingulum. **7**, antero-labial accessory cusp displaced medially. **8**, upper postcanines very compressed mesio-distally. **9**, development of a central basin; apparition of one antero-lingual accessory cusp. **10**, transverse ridge concave backwards; geniculate outline of the upper postcanines.

Rosieria delsatei n.sp.
(Figs 27, 28)

HOLOTYPE. — IRSNB R173, an upper left postcanine, root not preserved.

DERIVATIO NOMINIS. — Dedicaced in honour to Dr. D. Delsate, for his active palaeontological field-work in Lorraine and adjacent areas.

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

STRATUM TYPICUM. — "Rhaetian" sandstones. Upper Triassic.

DIAGNOSIS. — Traversodontidae known by one upper postcanine tooth, with the following characters: crown very small (width = 1.22 mm) with a subrectangular outline, in occlusal view (ratio "length/width" of the crown = 2.2); labial side straight and lingual side convex. Main lingual cusp much higher than the labial one. Transverse ridge set behind the middle of the crown: it does not participate in the posterior wall of the crown; anterior basin consequently much larger than the posterior basin. No central cusp on the transverse ridge. Small antero-labial accessory cusp connected to the main labial cusp by a prominent ridge. Both anterior and posterior cingula not developed.

DESCRIPTION

Orientation

The orientation of IRSNB R173 proposed here is mainly based on the presence of an accessory cusp, assumed to be set in antero-labial position, as in the advanced Traversodontidae (see Battail 1989, fig. 123). If this orientation is correct, the lingual side of the crown is more convex than the labial one, as in most Traversodontidae, and the lingual cusp is clearly higher than the labial one, as in *Traversodon* von Huene, 1936, *Scalenodon angustifrons* (Parrington, 1946), or *Microscalenodon* Hahn, Lepage *et* Wouters, 1988.

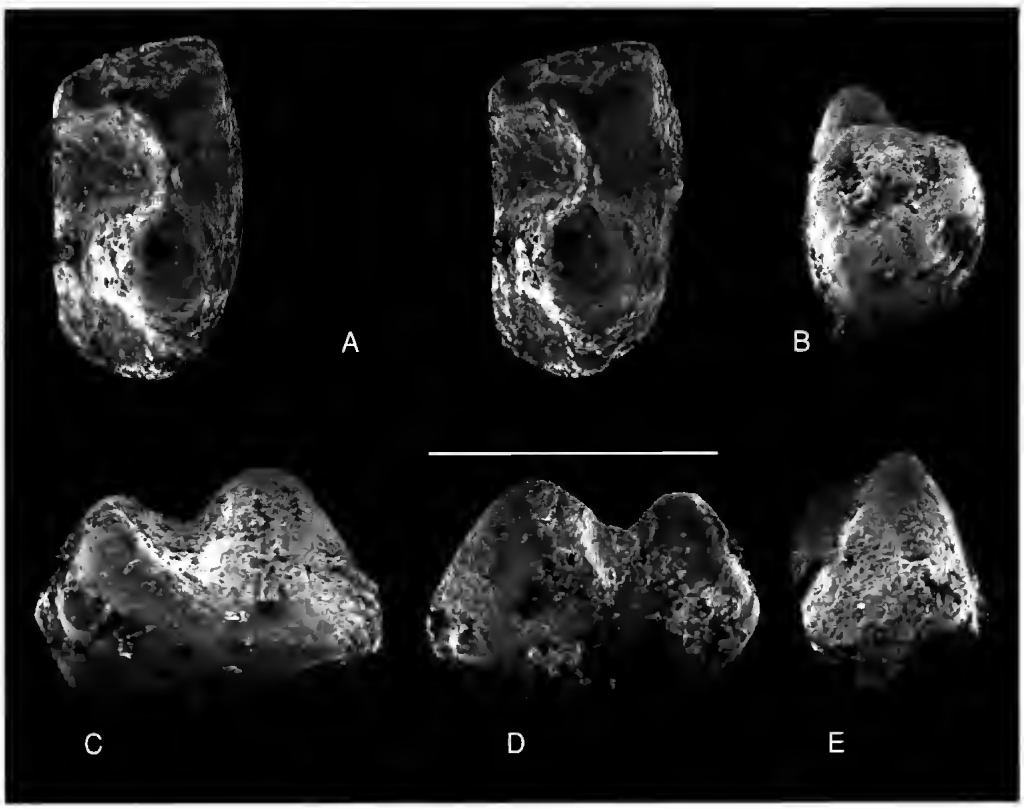

FIG. 27. — IRSNB R173, left upper postcanine of *Rosieria delsatei*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, stereophotographs, occlusal view; **B**, labial view; **C**, anterior view; **D**, posterior view; **E**, lingual view. Scale bar: 1 mm.

Moreover, the transverse ridge is set behind the middle part of the crown, as in all advanced Traversodontidae. Thus, IRSNB R173 is a left upper postcanine.

Measurements

Length of the crown = 0.55 mm; width of the crown = 1.22 mm.

Crown

The crown of IRSNB R173 is very small. In occlusal view, it is elongated (ratio "length/width" of the crown = 0.45) and subrectangular in outline. The labial border is nearly straight, whereas the lingual border is very convex. Both the anterior and posterior borders are slightly concave and nearly parallel. The crown is formed by two main cusps connected by a cutting transverse ridge. The main lingual cusp is much larger than the labial one. The transverse ridge is set behind the middle of the crown and does not support any central cusp. This ridge delimits a large anterior basin and a small posterior basin. A small antero-labial cusp is connected to the main labial cusp.

In labial view, the main and the accessory labial cusps are connected by a high ridge: their limit is not clear. The main labial cusp is clearly higher than the accessory one. Their apex is very rounded.

In lingual view, the lingual cusp has a piriform outline. Its base is very broad and both its anterior and posterior borders are sigmoid. Its apex is rounded.

In anterior view, both the labial and lingual borders of the crown are very convex. The lingual cusp is much wider and higher than the main labial cusp. The transverse ridge connecting these cusps is very high and its anterior wall is not as vertical as the posterior one. The anterior basin is not limited by an anterior cingulum.

In posterior view, the posterior wall of the trans-

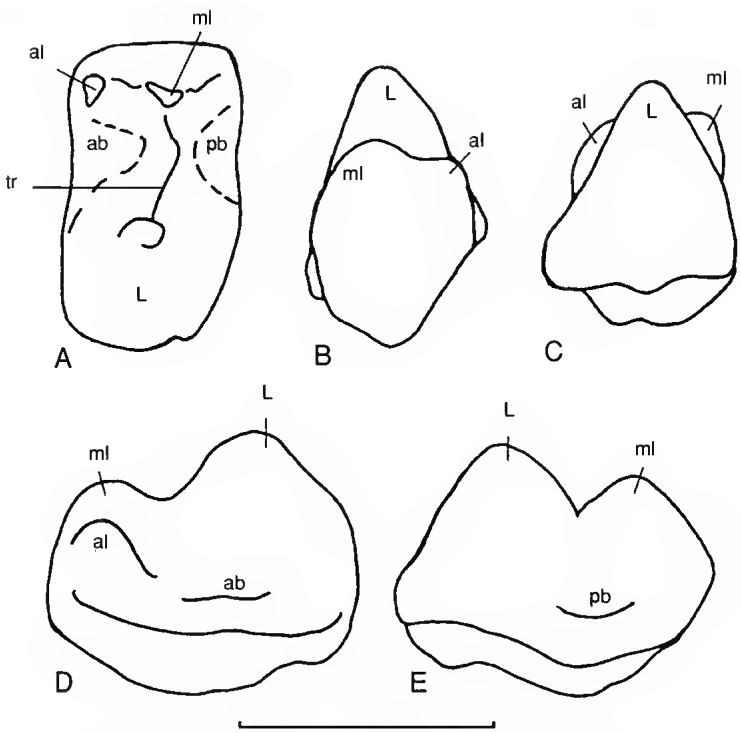

FIG. 28. — IRSNB R173, left upper postcanine of *Rosieria delsatei*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **ab**, anterior basin; **al**, antero-labial cusp; **L**, lingual cusp; **ml**, main labial cusp; **pb**, posterior basin; **tr**, transverse ridge. Scale bar: 1 mm.

verse ridge connecting the lingual and the main labial cusps is nearly vertical. The posterior basin, very poorly developed, forms a small depression at the level of the junction between the lingual and the labial cusps; it is not limited posteriorly by a posterior cingulum. A constriction delimits the crown and the root.

Root
The root is not preserved in IRSNB R173.

DISCUSSION
IRSNB R173 differs from IRSNB R172, referred to the new species *Maubeugia lotharingica*, in its proportionally wider outline, in its lingual cusp much higher than its main labial cusp and in lacking a central cusp. Moreover, the antero-labial accessory cusp is clearly less developed than in the latter: however, the development of this cusp is highly variable in the tooth row of the Traversodontidae (see Crompton 1972).
It resembles IRSNB R406, discovered in the Rhaetian of Habay-la-Vieille and referred to *Microscalenodon nanus* Hahn, Lepage *et* Wouters, 1988, in its small size, in its proportionally wide crown, in its lingual cusp much higher than its labial cusp and in lacking a central cusp. It differs from the latter in retaining a small posterior basin and an antero-labial accessory cusp.
IRSNB R173 resembles the upper postcanine teeth of *Scalenodon angustifrons* (Parrington, 1946), from the Middle Triassic of Tanzania, in the elongated outline of its crown, in its lingual cusp clearly higher than its labial one, in the presence of an antero-labial accessory cusp, in its transverse ridge set posteriorly, behind the middle of the crown, and in retaining a small posterior basin. It differs, however, from the latter in its smaller size and in lacking a central cusp as well as a cingulum.
The new tooth from Saint-Nicolas-de-Port resembles the upper postcanines of *Traversodon* von Huene, 1936 in its lingual cusp much higher than its labial cusp, in the absence of accessory cusp and in the presence of a posterior basin distinctly smaller than the anterior one. It differs in its smaller size and in the presence of a well developed antero-labial accessory cusp, absent in *Traversodon*. Moreover, the transverse ridge seems set more posteriorly in IRSNB R173.
Contrary to the upper postcanine teeth of *Massetognathus* Romer, 1967, *Gomphodontosuchus* von Huene, 1928, *Ischignathus* Bonaparte, 1963, *Exaeretodon* Cabrera, 1943, *Boreogomphodon* Sues *et* Olsen, 1990 and *Arctotraversodon* Sues, Hopson *et* Shubin, 1992, the transverse ridge of IRSNB R173 does not form the posterior wall of the crown and the anterior basin is consequently less enlarged than in the former genera.

In conclusion, the crown of IRSNB R173 presents an original set of characters justifying its attribution to a new genus of Traversodontidae: *Rosieria*. Figure 26 shows that the upper postcanines of *Roseria* can easily be derived from those of *Traversodon* by simple addition of an antero-labial accessory cusp and by slight backwards movement of the transverse ridge. In the same way, the postcanine teeth of *Scalenodon* and *Maubeugia* can be derived from those of *Rosieria*, by doubling of the lingual or the labial cusp, respectively.

Genus aff. *Roseria*
(Figs 29, 30)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R174, a left upper postcanine.

DESCRIPTION
Orientation
As in IRSNB R173.

Measurements
Length of the crown = 0.65 mm; width of the crown = 1.05 mm.

Crown
In occlusal view, the crown is very elongated labio-lingually (ratio "length/width" of the crow = 0.62) and subelliptical in outline. The lingual border is more convex than the labial one and the anterior border, much more convex than the posterior one: the latter is nearly perfectly straight. The crown is formed by two cusps

connected together by a transverse ridge. The lingual cusp is much larger than the labial one. The transverse ridge is relatively low, in the middle of the crown. It is set behind the middle of the crown and does not support any central cusp. This transverse ridge delimits a small posterior basin and a larger anterior basin. The posterior basin is limited posteriorly by a low, poorly developed and straight posterior cingulum. The anterior cingulum limiting the anterior basin is very poorly expressed, too, but very convex. There is no evidence of an accessory cusp.

In lingual view, the lingual cusp has a piriform outline: its base is broad and its apex rounded. Its anterior border is slightly concave, but its posterior border is nearly straight. There is no clear constriction between the crown and the root.

In labial view, the labial cusp has a triangular outline: both its anterior and posterior borders are nearly straight. Its posterior border is more oblique than its anterior border. Its apex is rather rounded.

In anterior view, the lingual cusp is much wider and somewhat higher than the labial one. The

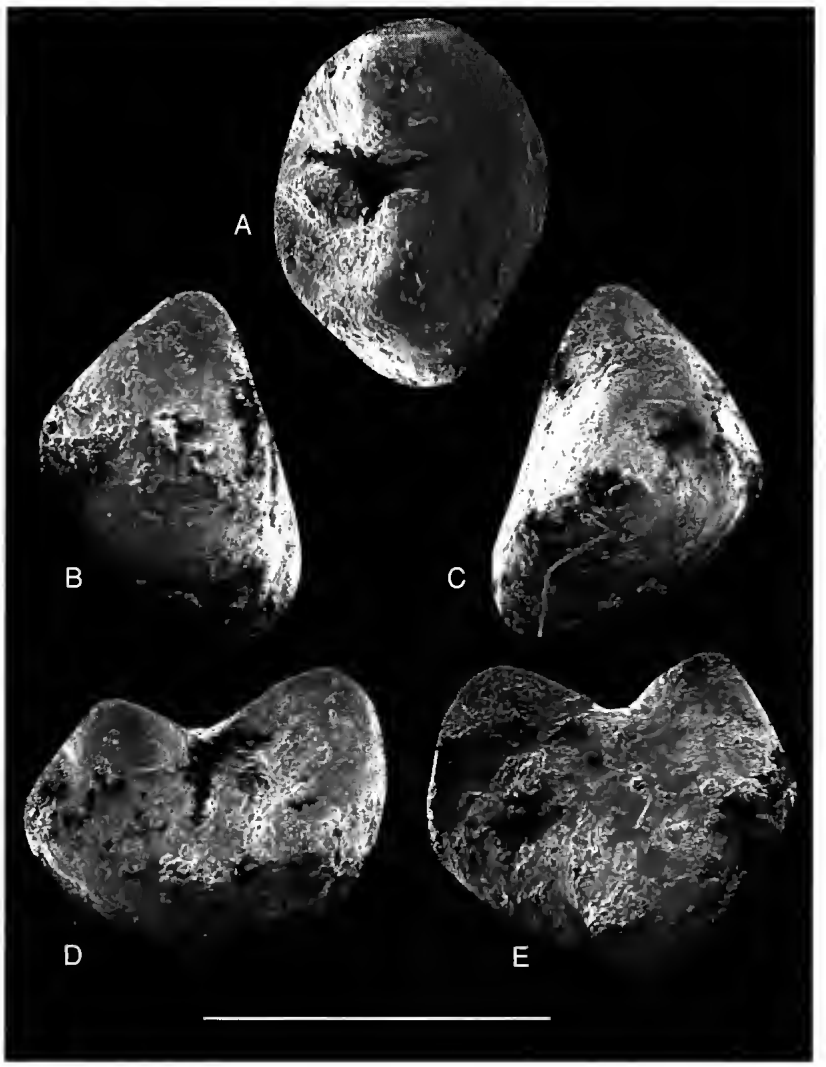

FIG. 29. — IRSNB R174, left upper postcanine of aff. *Rosieria*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. Scale bar: 1 mm.

transverse ridge forms a deep notch, at the level of the junction between these cusps. The slope of the anterior wall of the transverse ridge is not very marked. The anterior cingulum is very low. In posterior view, the posterior basin looks very small. The posterior wall of the transverse ridge is more vertical than the anterior one. The posterior cingulum is very short and very low.

Root

The root of IRSNB R174 is robust, but very eroded. It was at least 1.5 times as high as the crown. In lingual view, it has a semielliptical outline. Its vertical axis is oblique, set at an angle of about 30° with the vertical axis of the crown. Its anterior side is more convex than its posterior one. In anterior view, the root has a triangular outline. Both its labial and lingual sides are slightly convex. The lingual side is longer than the labial one. The tip of the root is very rounded and set at the level of the junction between the cusps of the crown.

Discussion

IRSNB R174 is reminiscent of IRSNB R173, referred to the newly defined species *Rosieria delsatei*, in its small and elongated crown, in its lingual cusp larger and higher than its labial one, in its transverse ridge set behind the middle of the crown, without central cusp, and in the retention of a small posterior basin. It differs mainly in the absence of a small antero-labial accessory cusp. In this character, it rather resembles *Traversodon*. However, the absence of this accessory cusp on an isolated tooth is, in advanced Traversodontidae, a negative character without actual phylogenetical significance. In *Scalenodon*, for example, the development of the anterior accessory cusps and of the cingula is variable within the dental row of a same animal (see Crompton 1972). For this reason, it cannot be excluded that IRSNB R174 belongs to the same species or, at least, to the same genus as IRSNB R173. That is the reason why the former postcanine is provisionally referred to aff. *Rosieria*, waiting for further evidence.

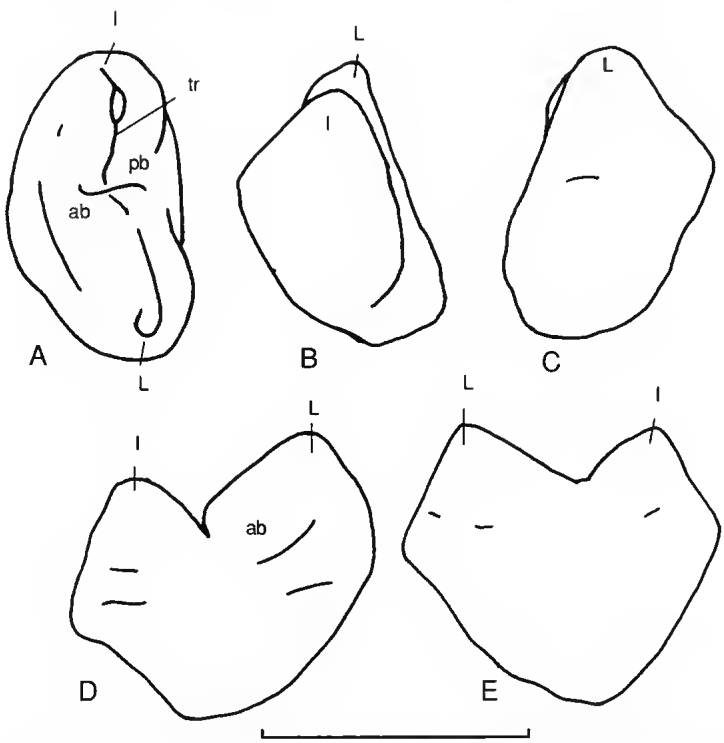

Fig. 30. — IRSNB R174, left upper postcanine of aff. *Rosieria*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **ab**, anterior basin; **L**, lingual cusp; **I**, labial cusp; **pb**, posterior basin; **tr**, transverse ridge. Scale bar: 1 mm.

Genus aff. *Microscalenodon*
(Figs 31, 32)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R175, a left upper postcanine.

DESCRIPTION

Orientation

See Hahn, Lepage & Wouters 1988.

Measurements

Length of the crown: 0.58 mm; width of the crown: 1.15 mm.

Crown

In occlusal view, the crown is proportionally very wide (ratio "length/width" of the crown = 0.5) and subrectangular in outline. The labial border is shorter and more convex than the lingual one, which is an unusual character in the Traversodontidae. The posterior border is perfectly straight and the anterior border, somewhat convex. The morphology of the crown is quite simple: two cusps connected together by very poorly developed anterior and posterior ridges ("cingula"). The lingual cusp is by far the largest; the labial cusp is very short antero-posteriorly, but rather elongated labio-lingually. The ridges delimit a large central basin. There is no evidence of a transverse ridge: it is merged probably with the posterior ridge, forming the posterior wall of the crown. There is neither central nor accessory cusps.

In lingual view, the lingual cusp is not very high and has a piriform outline: its base is large antero-posterioly and its apex is very rounded.

In labial view, the labial cusp is very low and triangular in outline. It clearly slopes towards the anterior side. Its apex is rounded, too.

In anterior view, the lingual cusp is distinctly higher than the labial cusp. The anterior ridge is nearly non-existent. The central basin gently slopes from the posterior wall to the anterior base of the crown.

In posterior view, the posterior ridge is clearly higher than the anterior one and forms the posterior wall of the crown.

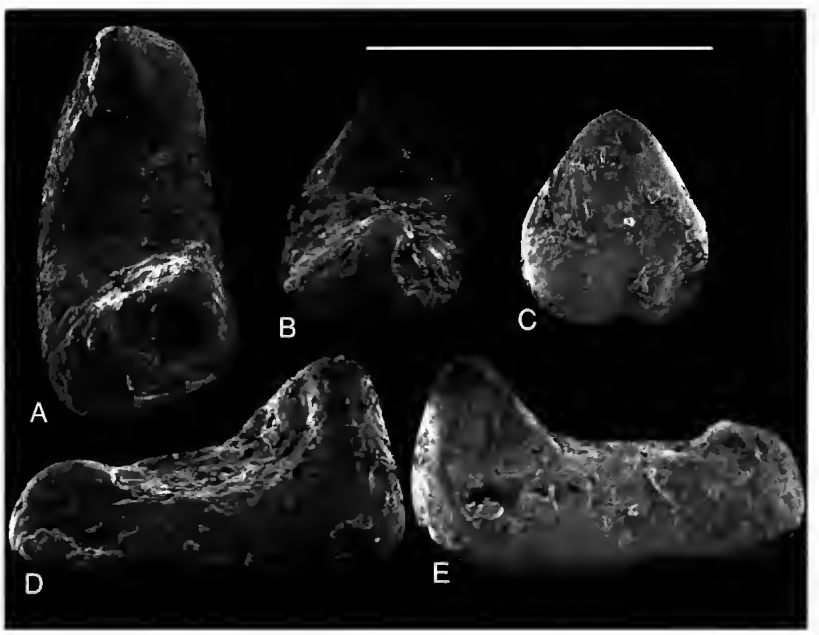

FIG. 31. — IRSNB R175, left upper postcanine of aff. *Microscalenodon*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. Scale bar: 1 mm.

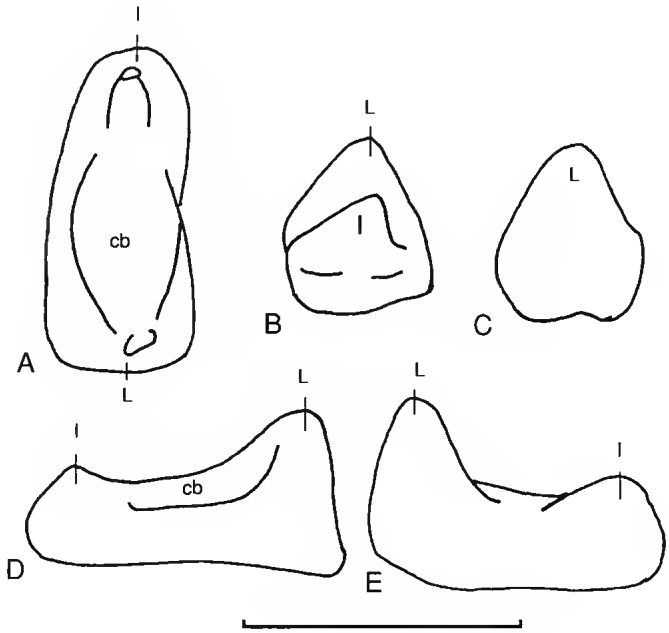

FIG. 32. — IRSNB R175, left upper postcanine of aff. *Microscalenodon*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **cb**, central basin; **L**, lingual cusp; **I**, labial cusp. Scale bar: 1 mm.

Root

The root is not preserved in this specimen.

DISCUSSION

IRSNB R175 resembles *Microscalenodon nanus* Hahn, Lepage *et* Wouters, 1988 in the quite simple structure of its crown, without transverse ridge, central and accessory cusps. Moreover, the anterior and the posterior sides of the crown are nearly parallel, the lingual cusp is very rounded and the central basin gently slopes from the posterior wall to the anterior base of the crown. It differs from IRSNB R406, the holotype and only upper postcanine currently referred to *Microscalenodon nanus*, in its crown proportionally lower, in its labial cusp less developed and in lacking an extended wear facer on its occlusal side. In the current state of our knowledge, for want of material, we cannot form a correct estimate of the dental variation within the species *Microscalenodon nanus*. That is the reason why IRSNB R175 is tentatively referred to aff. *Microscalenodon*.

Family TRAVERSODONTIDAE, gen. and sp. indet.
(Figs 33, 34)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R176, a left lower postcanine.

DESCRIPTION

Orientation

In the Traversodontidae, the lower postcanines are formed by a transverse ridge supporting two main cusps on the anterior half of the crown and by a low basin on the posterior half of the crown. The labial main cusp is usually higher than the lingual one.

Measurements

Length of the crown = 1.32 mm; width of the crown = 1.13 mm.

Crown

In occlusal view, the crown has a subtrapezoidal outline. It is proportionally longer than wide: the

ratio "length/width" of the crown = 1.17. The posterior half of the labial border and the posterior border are very convex. The lingual border is nearly perfectly straight. The anterior border is slightly concave and very oblique. The anterior half of the crown is formed by two large cusps connected together by an anterior transverse ridge. The labial cusp is much longer (mesio-distally), but somewhat less wide (labio-lingually) than the lingual cusp. In front of the transverse ridge, the labial cusp bears a poorly developed swelling. A tiny anterior depression is limited by the anterior wall of the transverse ridge and by the lingual side of the anterior swelling of the labial cusp. The posterior half of the crown forms a talon, not very large and distinctly narrower than the anterior part of the crown. The posterior talon forms a central valley elongated antero-posteriorly and surrounded by a ridge which bears a broad lingual accessory cusp, adjoining the main lingual cusp.

In anterior view, the crown has a bell-shaped outline. The labial cusp is distinctly higher than the lingual cusp. The transverse ridge connecting these cusps is not very high. The anterior depression has a triangular outline. The crown and the root are separated by a well marked constriction.

In posterior view, the central valley of the poste-

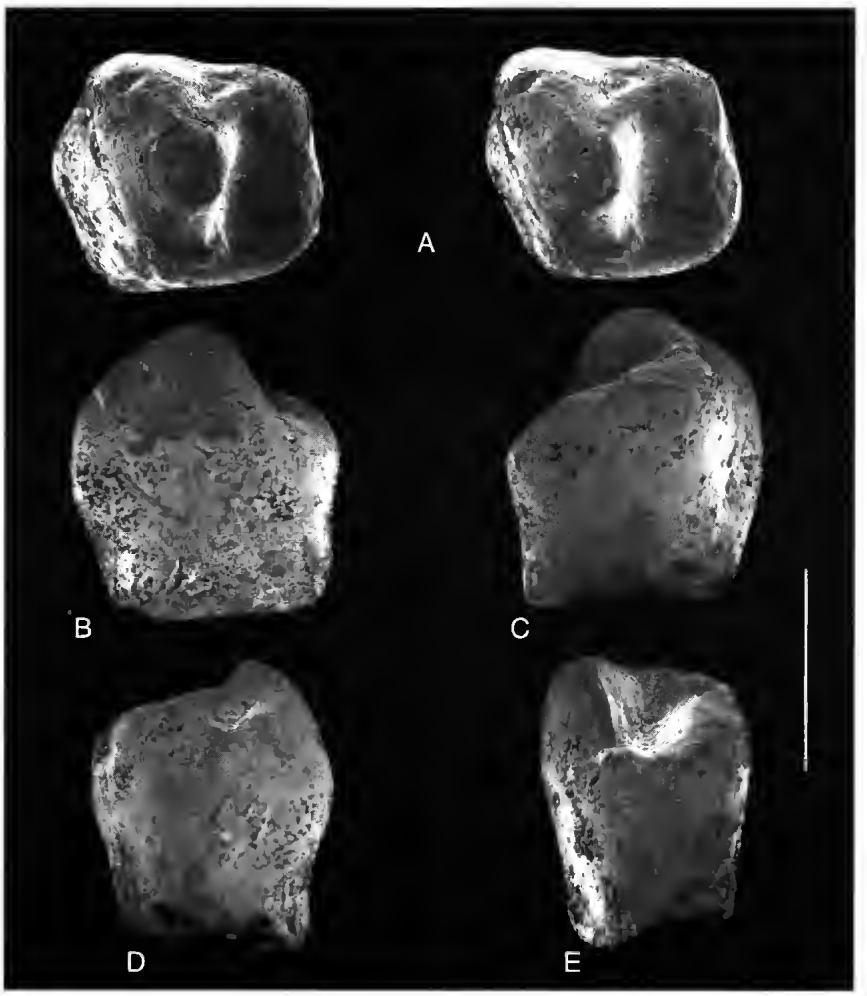

FIG. 33. — IRSNB R176, left lower postcanine of Traversodontidae indet., from the Late Triassic of Saint-Nicolas-de-Port. **A**, stereophotographs, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. Scale bar: 1 mm.

rior talon gently slopes from the transverse ridge to the posterior wall of the crown. The posterior portion of the ridge surrounding the valley is particularly low.

In labial view, the large labial cusp has a triangular outline. It is broader than high. Its anterior border is convex; its posterior border is shorter and straight. Therefore, this cusp somewhat slopes backwards. Its apex is very eroded. The lingual part of the talon looks proportionally very short. The crown is separated from the root by a well marked constriction, as in anterior view.

In lingual view, the main and the accessory lingual cusps are so closely united and their apex are so eroded that they form a quasi-continuous and straight ridge which slopes obliquely downwards from the main to the accessory cusp. The anterior swelling of the labial cusp lies in front of the level of the anterior border of the main lingual cusp.

Root

The tip of the root is broken. At the level of the fracture, the root has, in basal view, an ovoid outline. Its anterior border is shorter, but more convex than its posterior border; its lingual border is more convex than its labial border. The pulpal canal is very small and rounded.

Discussion

IRSNB R176 has the typical traversodont pattern of a transverse ridge supporting two main cusps on the anterior half of the crown and a narrower talon on its posterior half. If the upper postcanines are very variable and, thus, phylogenetically useful in the Traversodontidae, the lower postcanines are much more constant and less diagnostical.

The lower postcanines of the primitive Traversodontidae *Pascualgnathus* Bonaparte, 1966 and *Andescynodon*, Bonaparte, 1969 differ

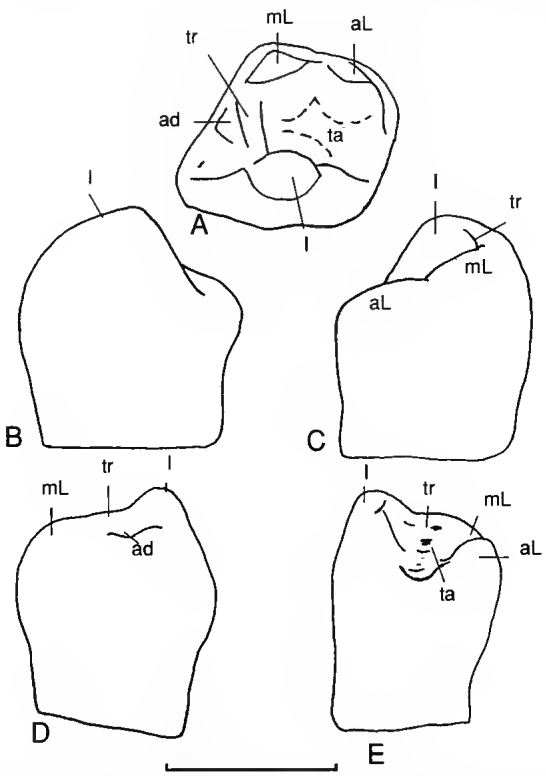

Fig. 34. — IRSNB R176, left lower postcanine of Traversodontidae ind., from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **ad**, anterior depression; **aL**, accessory lingual cusp; **I**, labial cusp; **mL**, main lingual cusp; **ta**, talonid; **tr**, transverse ridge. Scale bar: 1 mm.

from IRSNB R176 in the presence of a postero-labial accessory cusp, connected to the main labial cusp by a low ridge, and in the lack of a postero-lingual accessory cusp on the talon of their crown. Moreover, the posterior basin is more enlarged than in the latter. There is no trace of anterior swelling on the anterior side of the main labial cusp.

In the lower postcanines of *Scalenodon* Crompton, 1955, a small accessory cusp, equivalent to the anterior swelling of the labial cusp observed in IRSNB R176, is developed on the antero-labial side of the crown. However, a posterior accessory cusp is present on the labial side of the talon, rather than on the lingual side, as in IRSNB R176. Moreover, the posterior basin is more enlarged than in the latter.

In *Massetognathus* Romer, 1967, the posterior talon is lower and its basin is more enlarged than in IRSNB R176. Both the labial and lingual ridges of the talon are crenulated, but there is neither well developed posterior accessory cusp nor anterior swelling of the labial cusp.

The lower postcanines of *Gomphodontosuchus* von Huene, 1928, *Exaeretodon* Cabrera, 1943, *Ischignathus* Bonaparte, 1963 and *Scalenodontoides* Crompton *et* Ellenberger, 1957 differ from IRSNB R176 in possessing the following derived characters:

– The lingual cusp is distinctly inclined obliquely backwards.
– The labial cusp is broader than the lingual cusp.
– Except in *Ischignathus*, the labial cusp is set anteriorly with respect to the lingual cusp.
– There are two accessory cusps: a postero-lingual one and a postero-labial one.

The lower postcanine referred to *Microscalenodon nanus* Hahn, Lepage *et* Wouters, 1988 resembles IRSNB R176 in its very small size and in the proportions of its main cusps. Nevertheless, an accessory cusp is developed on the postero-labial side of the crown, the talon and the posterior basin are distinctly more developed and the labial cusp does not bear any anterior swelling.

From these comparisons with the lower postcanines in the different genera of Traversodontidae, it can be concluded that IRSNB R176 shows an original set of morphological characters:

– The antero-labial cusp is longer (mesio-distally) but less wide (labio-lingually) than the antero-lingual cusp.
– The antero-labial cusp supports an anterior swelling.
– There is a broad postero-lingual accessory cusp.
– The talon is not very enlarged: it forms a central valley elongated antero-posteriorly.
– The tooth is very small.

In the absence of more complete material, correspondences with the genera *Maubeugia* and *Rosieria*, defined on isolated upper postcanines from the same locality, are impossible to establish. That is the reason why IRSNB R176 is referred to Traversodontidae indet.

Family aff. TRAVERSODONTIDAE, gen. and sp. indet. (Figs 35, 36)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R177.

DESCRIPTION

Orientation

IRSNB R177 shows morphological affinities with the upper postcanines of the Traversodontidae (see discussion). The marked slope of the main cusps permits to distinguish the anterior and posterior sides of the crown. If the interpretation proposed here is correct, the small accessory cusp would be set on the antero-labial border of the crown, as in advanced Traversodontidae. Therefore, it is identified as a right upper postcanine.

Measurements

Length of the crown = 1.39 mm; width of the crown = 1.5 mm.

Crown

In occlusal view, the crown of IRSNB R177 is subtrapezoidal and very elongated antero-posteriorly: the ratio "length/width" of the crown is 0.93. The lingual border is long and very convex;

the labial one is shorter and slighrly concave. Both the anterior and posterior borders are nearly straight and oblique: the posterior border is longer than the anterior one. The crown is divided into two parts by an antero-posterior furrow. The lingual part is the widest and is fully covered by a very large lingual cusp. The labial side of the crown is formed by two labial cusps. The posterior labial cusp is the largest: it is connected to the apex of the labial cusp by a transverse ridge, set behind the middle of the crown. The antero-labial accessory cusp is connected to the main labial cusp by a small ridge and connected to the lingual one by a poorly developed anterior cingulum. The transverse ridge, connecting the lingual and the main labial cusps, delimits an anterior and a posterior valley. The anterior valley is surrounded by the antero-labial side of the lingual cusp, the anterior wall of the transverse ridge, the antero-lingual side of the main labial cusp, the lingual side of the accessory labial cusp and the posterior wall of the anterior cingulum. The posterior valley is distinctly smaller than the anterior one: it is limited by the postero-labial side of the lingual cusp, the posterior wall of the transverse ridge and the postero-lingual side of the main labial cusp. There is no evidence of a posterior cingulum.

In anterior view, the lingual cusp is by far the highest: the main labial cusp reaches the half of its height and the accessory labial cusp, the third of the main labial cusp. Both the lingual and the main labial cusps are somewhat inclined towards the labial side of the crown. The transverse ridge is deeply notched by the antero-posterior furrow. The anterior cingulum is very low and is also notched by the antero-posterior furrow. The postero-lingual side of the main labial cusp is less vertical than the antero-labial side of the lingual cusp.

In posterior view, the postero-labial side of the main cusp is nearly perfectly vertical; the postero-lingual side of the main labial cusp is more oblique. The posterior valley is opened posteriorly: it is not limited by a posterior cingulum. The posterior ridge of the lingual cusp is well marked.

In lingual view, the lingual cusp is subtriangular in outline and clearly inclined backwards. The anterior border is oblique, forming an angle of about 45° with the base of the crown, and somewhat convex. The posterior border is shorter, more vertical and very slightly concave. The apex of the cusp is very rounded.

In labial view, the main labial cusp has almost

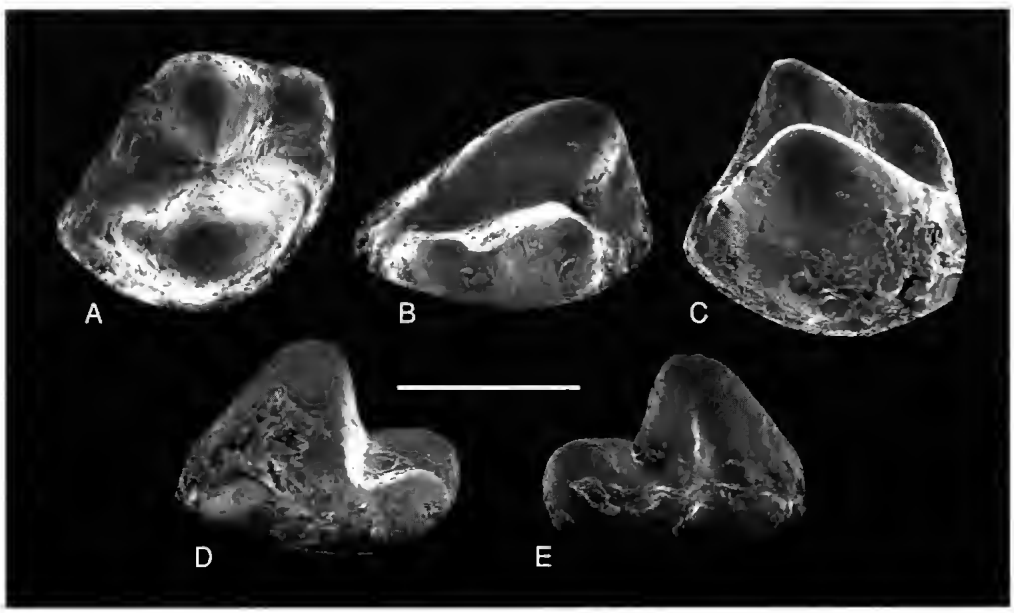

Fig. 35. — IRSNB R177, right upper postcanine of ? Traversodontidae indet., from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. Scale bar: 1 mm.

the same outline as the lingual cusp. It is inclined backwards and its apex is rounded too. The accessory labial cusp, very low, is placed against it: the ridge connecting the two labial cusps is low and poorly developed.

Root.
The root is not preserved in IRSNB R177.

DISCUSSION
IRSNB R177 is undoubtedly reminiscent of the upper postcanine teeth of the advanced Traversodontidae in the general organisation of its crown. A large lingual cusp is connected to the main accessory cusp by a transverse ridge set behind the middle of the crown and delimiting an anterior and a smaller posterior valley. An accessory cusp is set in front of the main labial cusp and the anterior valley is closed by an anterior cingulum. The organisation of the cusps is similar to IRSNB R174, referred to the newly defined genus *Rosieria*. Nevertheless, it differs from the upper postcanines of all currently known Traversodontidae in being longer (mesio-distally) than wide (labio-lingually).
In its proportions, IRSNB R177 more closely resembles the lower postcanines of the Traversodontidae. Nevertheless, its morphological organization is quite different. The lower postcanines of the Traversodontidae are rather constant indeed (see Battail 1989): a high transverse ridge supports two cusps on the anterior half of the crown and a low basin forms the posterior half. An accessory cusp is usually present on the postero-labial portion of the crown.
In certain respects, IRSNB R177 is reminiscent of the postcanine of the Haramiyidae. This group, only known by isolated teeth, is very abundant in Saint-Nicolas-de-Port (Sigogneau-Russell 1989, 1990). The Haramiyidae are tentatively identified as primitive allotherian mammals (see Butler & Macintyre 1994 for an extended discussion of Haramiyidae affinities). As in IRSNB R177, the dental crowns of the Haramiyidae are elongated antero-posteriorly and they are divided into two rows of cusps by a deep antero-posterior furrow. However, the "accessory cusps" are more numerous on the anterior part of the lower postcanines and on the posterior part of the upper ones. Moreover, the posterior slope of the dominating cusps is never as marked as in IRSNB R177.

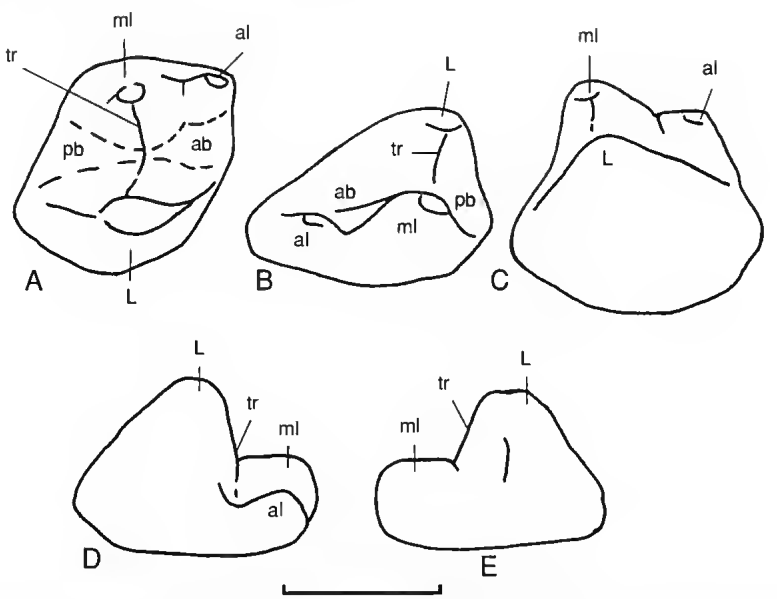

FIG. 36. — IRSNB R177, right upper postcanine of ? Traversodontidae indet., from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **ab**, anterior basin; **al**, antero-labial cusp; **L**, lingual cusp; **ml**, main labial cusp; **pb**, posterior basin; **tr**, transverse ridge. Scale bar: 1 mm.

It can be concluded that IRSNB R177 most closely resembles the upper postcanines of the Traversodontidae: the general organization of the cusps is similar to the new defined genus *Rosieria*. Because of its very unusual proportions, it is cautiously referred to familia aff. Traversodontidae, waiting for the discovery of more complete material.

PALAEOBIOGEOGRAPHY OF LATE TRIASSIC AND EARLY JURASSIC CYNODONTS

FOSSIL LOCALITIES AND HORIZONS

Table 9 gives a synthetic correlation, modified from Lucas & Hunt (1994), of Late Triassic and Early Jurassic formations discussed in the text.

Ischigualasto Formation
(San Juan Province, Argentina)
Age. Late Carnian (Hunt 1991; Hunt & Lucas 1991). Early to Late Carnian (Battail 1993).
Taxa discovered. Traversodontidae: *Exaeretodon frenguelli* Cabrera, 1943; *Exaeretodon vincei* (Bonaparte, 1963); *Ischignathus sudamericanus* (Bonaparte, 1963).
Chiniquodontidae: *Chiniquodon theotonicus* von Huene, 1936.

Upper part of the Los Colorados Formation
(La Rioja Province, Argentina)
Age. Late Norian (Bonaparte 1972; Lucas & Hunt 1994).
Taxa discovered. Tritheledontidae: *Chaliminia musteloides* Bonaparte, 1978.
Remark. Bonaparte (1972) identified postcranial bones as cf. *Tritylodon*. Lucas & Hunt (1994) suspect that they pertain to *Chaliminia*.

Upper Santa Maria Formation
(Rio Grande do Sul, Brazil)
Age. Late Carnian (Hunt 1991; Hunt & Lucas 1991). Early Carnian (Battail 1993).
Taxa discovered. Traversodontidae: *Traversodon stahleckeri* von Huene, 1936; *Gomphodontosuchus brasiliensis* von Huene, 1928; *Exaeretodon frenguelli* Cabrera, 1943.
Dromatheriidae: *Therioherpeton cargnini* Bonaparte *et* Barberena, 1975.
Chiniquodontidae: *Chiniquodon theotonicus* von Huene, 1936; *Belesodon magnificus* von Huene, 1936.

Lower Elliot Formation
(Morobong Hill, Lesotho)
Age. Late Carnian or Early Norian (Hopson 1984).
Taxon discovered. Traversodontidae: *Scalenodontoides macrodontes* Crompton *et* Ellenberger, 1957.

Upper Elliot and Clarens Formations
(South Africa and Lesotho)
Age. Hettangian to Sinemurian (Olsen & Galton 1984).
Taxa discovered. Tritheledontidae: *Pachygenelus monus* Watson, 1913; *Diarthrognathus broomi* Crompton, 1958; *Tritheledon riconoi* Broom, 1912.
Tritylodontidae: *Tritylodon longaevus* Owen, 1884 (*sensu* Sues 1986b).
Remark. *Pattsia likhoelensis* Lees *et* Mills, 1983, from Lesotho, is certainly a Tritheledontidae, possibly a synonym of *Pachygenelus monus* (Lucas & Hunt 1994).

Maleri Formation
(Andhra Pradesh, India)
Age. Late Carnian (Hopson 1984; Battail 1991).
Taxon discovered. Traversodontidae: *Exaeretodon statisticae* Chatterjee, 1982.
Remark. Battail (1991) considers that *Exaeretodon statisticae* might be a junior synonym of *Exaeretodon frenguelli*.

Bull Canyon Formation
(Eastern New Mexico, USA)
Age. Early to Middle Norian (Lucas & Hunt 1994, fig. 20.5).
Taxon discovered. Dromatheriidae: *Pseudotriconodon chatterjeei* Lucas *et* Oakes, 1988.
Remark. The identification of this taxon as a cynodont has been questioned by Sues & Olsen (1990), but without justification.

Kayenta Formation
(North-eastern Arizona, USA)
Age. Late Sinemurian – Early Pliensbachian

	SERIES	Stage	Argentina	Brazil	Southern Africa	India	Western North Amer.	Eastern North Amer.	United Kingdom	France	Belgium Luxemb.	Switzer-land	Germany	China
178	EARLY JURASSIC	Toarcian												
187		Pliens-bachian					Navajo Ss. 10		Windsor Hill Fissure 16					
194,5		Sinemurian			Upper Elliot and Clarens Fm 5		Kayenta Fm 8 / La Boca Fm 9		St. Brides's Island 15					Lufeng Fm 22
203,5		Hettan-gian						Mc Coy Brook Fm 14						
208		Rhaetian									Habay-l.-V. 19	Hallau Bone-bed 20	Rhätsanstein 21	
210	UPPER TRIASSIC	Norian	Los Colorados Fm 2				Bull Canyon Fm 7			St.-Nicolas de-Port 17	Medernach 18			
222		Carnian	Ischigualasto Fm 1	Upper Santa Maria Fm 3	Lower Elliot Fm 4	Maleri Fm 6		Cumnock 12 / Wolfville Fm 13 / Turkey Barnch Fm 11						
229														

TABLE 9. — Stratigraphic position of the Late Triassic and Early Jurassic formations where cynodonts have been discovered (after Lucas & Hunt 1994, modified).

(Peterson & Pipiringos 1979; Clark & Fastovsky 1986; Sues 1986b).
Taxa discovered. Tritylodontidae: *Kayentatherium wellesi* Kermack, 1982; *Oligokyphus* sp.; *Dinnebitodon amarali* Sues, 1986; *Nearctylodon broomi* Lewis, 1986.

La Boca Formation
(Tamaulipas, north-eastern Mexico)
Age. ? Early Jurassic (Clark *et al.* 1991, 1994). New radiometric datas indicate that this formation would be Middle Jurassic in age (Luo, pers. comm.).
Taxon discovered. Tritylodontidae: *Bocatherium mexicanum* Clark *et* Hopson, 1985.

Navajo Sandstones
(Arizona, USA)
Age. Pliensbachian (Marzolf 1990).
Taxon discovered. Tritylodontidae: Tritylodontid indet. (Winkler *et al.* 1991).

Turkey Branch Formation
(Richmond Basin,Virginia, U.S.A.)
Age. Early to Middle Carnian (Sues & Olsen 1990; Sues *et al.* 1994).
Taxa discovered. Traversodontidae: *Boreogomphodon jeffersoni* Sues *et* Olsen, 1990.
Dromatheriidae: *Microconodon tenuirostris* Osborn, 1886.

Cumnock Formation
(Sanford Basin, North Carolina, USA)
Age. Late Carnian (Sues *et al.* 1994; Lucas & Hunt 1994).
Taxa discovered. Dromatheriidae: *Dromatherium sylvestre* Emmons, 1857; *Microconodon tenuirostris* Osborn, 1886.

Wolfville Formation of the Fundy Group
(Minas Basin, Nova Scotia, Canada)
Age. Late Carnian or Carno-Norian (Hopson 1984).
Taxon discovered. Traversodontidae: *Arctotraversodon plemmyridon* (Hopson, 1984).

Mc Coy Brook Formation of the Fundy Group
(Novia Scotia, Canada)
Age. Early Jurassic (Shubin *et al.* 1991): ? Hettangian (Lucas & Hunt 1994).
Taxon discovered. Tritheledontidae: *Pachygenelus* cf. *monus*.
Remark. ? *Pachygenelus milleri* Chatterjee, 1983, from the Dockum Formation (Upper Triassic) of Near Post (Western Texas, USA) is regarded by Shubin *et al.* (1991) as doubtful because it lacks diagnostic cynodont characters: teeth are fused to the jaw and there are no cingula on the post-canine teeth.

Pant 4 Quarry of St. Bride's island
(Glamorgan, U.K.)
Age. Hettangian to Early Sinemurian (Evans & Kermack 1994).
Taxon discovered. Tritylodontidae: *Oligokyphus* cf. *major*.

Windsor Hill Fissure
(Somerset, UK)
Age. Pliensbachian (Kühne 1956).
Taxon discovered. Tritylodontidae: *Oligokyphus major* Kühne, 1956.
Remarks. Kühne (1956) described originally two species, *O. major* and *O. minor*, which are probably sexual dimorphs (Sues 1985).
A tritylodontid *incertae sedis* is present at the nearby Holwell Quarry (Savage 1971).

Saint-Nicolas-de-Port
(Meurthe-et-Moselle, France)
Age. Late Norian (Buffetaut & Wouters 1986; Cuny & Ramboer 1991; Cuny 1993) or Early Rhaetian (Sigogneau-Russell 1983a).
Taxa discovered. Dromatheriidae: *Pseudotriconodon wildi* Hahn, Lepage *et* Wouters, 1984; *Tricuspes tuebingensis* E. von Huene, 1933; *Tricuspes sigogneauae* Hahn, Hahn *et* Godefroit, 1994; *Tricuspes tapeinodon* n.sp.; *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994.
Traversodontidae: *Maubeugia lotharingica* n.g., n.sp.; *Rosieria delsatei* n.g., n.sp.; genus aff. *Microscalenodon*.
Cynodontia *incertae sedis*: *Hahnia obliqua* n.g., n.sp.; *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987; *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987.
Remark. Godefroit (1997) describes a Late Triassic fauna in the nearby and contempora-

neous locality of Varangéville. This fauna includes teeth of indeterminate advanced cynodonts.

Medernach
(G.-D. Luxemburg)
Age. ? Middle Norian (Hary & Muller 1967; Cuny *et al.* 1995).
Taxa discovered. Dromatheriidae: *Pseudotriconodon wildi* Hahn, Lepage *et* Wouters, 1984; "cf. *Tricuspes tuebingensis*" (= *Tricuspes* aff. *sigogneauae*).
Cynodontia *incertae sedis*: *Gaumia* cf. *incisa*.

Habay-la-Vieille
(Gaume, Belgium)
Age. Early Rhaetian (Bock 1987).
Taxa discovered. Dromatheriidae: *Pseudotriconodon* ? sp.
Traversodontidae: *Microscalenodon nanus* Hahn, Lepage *et* Wouters, 1988.
Cynodontia *incertae sedis*: *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987; ? *Gaumia incisa* Hahn, Wild *et* Wouters, 1987; *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987.

Hallau Bone-bed
(Kanton Schaffhausen, Switzerland)
Age. For Clemens (1980), the Hallau Bone-bed postdates the Upper Norian (Knolenmergel), but is no younger than the Lower, but not Lowermost, Hettangian (the bone-bed is overlain by a marl containing the ammonite *Psiloceras johnstoni*). Therefore, the Hallau local fauna is probably of Rhaetian age.
Taxa discovered. Dromatheriidae: *Tricuspes sigogneauae* Hahn, Hahn *et* Wouters, 1994.
Cynodontia *incertae sedis*: *Gaumia* sp.; *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987.

Rhätsandstein bone-beds of Württemberg
(Germany)
Age. Probably not older than Upper Norian and not younger than Lower Hettangian (Clemens 1980).
Taxa discovered. Dromatheriidae: *Tricuspes tuebingensis* E. von Huene, 1933.
Tritylodontidae: *Oligokyphus triserialis* Hennig, 1922 (*sensu* Sues 1985); *Tritylodon fraasi* Lydekker, 1887; *Chalepotherium plieningeri* (Ameghino, 1903).

Lower Lufeng Formation
(Western Yunnan, China)
Age. Hettangian to Pliensbachian (Chen *et al.* 1982; Luo & Wu 1995).
Taxa discovered. (according to Luo & Wu 1994). Tritylodontidae: *Bienotherium yunnanense* Young, 1940; *Bienotherium minor* Young, 1947; *Bienotherium magnum* Chow, 1962; *Oligokyphus lufengensis* Luo *et* Sun, 1993; *Lufengia delicata* Chow *et* Hu, 1959; *Yunnanodon brevirostre* (Cui, 1976); *Dianzhongia longistrata* Cui, 1981.

PALAEOGEOGRAPHICAL SKETCH OF ADVANCED CYNODONTS AND AFFINITIES OF THE SAINT-NICOLAS-DE-PORT CYNODONT FAUNA

Three successive stages can be distinguished in the Late Triassic and Early Jurassic cynodont assemblages worldwide: the Late Carnian/Early Norian assemblages, the Late Norian/Rhaetian assemblages and the Liassic assemblages. The Late Carnian/Early Norian assemblages are particularly well represented in South America (Argentina and Brazil), but elements have also been discovered in southern Africa, India and eastern North America. These assemblages are dominated by Traversodontidae. With the exception of *Boreogomphodon*, all are large or giant herbivorous cynodonts. The Chiniquodontidae apparently disappeared at the end of the Carnian. The Dromatheriidae appeared during the Carnian. They are very small cynodonts with perfectly sectorial postcanine teeth. This Late Carnian/Early Norian cynodont assemblages can be included within the B-type assemblages, defined by Romer (1966).

The Late Norian/Rhaetian cynodont assemblages are well represented in Western Europe, on the western margin of the Germanic Realm. The fauna discovered in Saint-Nicolas-de-Port is the most representative of this type of cynodont assemblages. These are dominated by small car-

nivorous or insectivorous cynodonts with sectorial postcanine teeth (Dromatheriidae or Cynodontia *incertae sedis*). The Traversodontidae are very rare and only represented by dwarf forms. The cynodont fauna from Saint-Nicolas-de-Port appears very similar with those from Medernach (three genera in common), Habay-la-Vieille (three or four genera in common) and Hallau (three genera in common).

From a palaeoecological point of view, it is interesting to observe that, in Saint-Nicolas-de-Port, small herbivorous Traversodontidae co-exist with two groups of herbivorous allotherian mammals: the Haramiyidae and the Theroteinidae. All these small herbivorous groups probably had different dietary specializations, allowing their sympathy. For Sigogneau-Russell & Hahn (1994), the haramiyid teeth, which are rarely strongly worn, may be indicative of a diet based on soft plant matter; the low cusps and delicate roots of the theroteinid molars perhaps suggest a diet based on rather softer vegetables. The stout root and the high cusps of the dwarf traversodontid postcanine teeth suggest a diet based on harder vegetables. The wear pattern of the postcanine teeth is unfortunately insufficiently known, in this group, to confirm this hypothesis. In the same way, the Dromatheriidae co-exist with morganucodontid mammals in Saint-Nicolas-de-Port, as in Hallau (Peyer 1956) and Medernach (Cuny *et al.* 1995). Both groups are characterized by triconodont cutting teeth and probably occupied similar ecological niches. Sigogneau-Russell & Hahn (1994) suggest that the Dromatheriidae ("chiniquodontoids") were probably too small to be carnivorous: perhaps they fed on insects with hard elytrae. In Saint-Nicolas-de-Port, the most frequent morganucodontid, *Brachyzostrodon*, is characterized by its relatively large and very stocky molars, indicating that it fed on larger preys: it was probably a small carnivorous.

The cynodont fauna discovered in the Rhätsandstein bone-beds from Germany has a intermediate composition between the typical Late Norian-Rhaetian assemblages and the Liassic ones. *Tricuspes* is the only dromatheriid discovered in this area, whereas at least three genera of tritylodontids have been discovered. These are the oldest Tritylodontidae currently recognized.

Outside Western Europe, the Late Norian Los Colorados Formation of Argentina has yielded the oldest known Tritheledontidae: *Chaliminia*. The presence of *Pseudotriconodon* in the Norian Bull Canyon Formation of New Mexico is doubtful (Sues & Olsen 1990).

Traversodontids and dromatheriids are absent from the Liassic cynodont assemblages. These are characterized by the presence of Tritylodontidae and/or Tritheledontidae. Liassic tritylodontids have a pangean palaeogeographical distribution: they are known from Europe, North America, China and South Africa. This reflects the apparent cosmopolitanism of tetrapod faunas at that period, as already noted by Shubin *et al.* (1981), Olsen & Galton (1984) and Lucas & Hunt (1994). Nevertheless, at the generic level, the Liassic tritylodontids appear more endemic. Out of ten tritylodontid genera recognized in the Early Jurassic (the Rhätsandstein bone-beds from Germany are provisionally regarded as Late Triassic in age), eight have currently only been discovered in a limited palaeogeographical area. *Dinnebitodon*, from the Kayenta Formation (USA), and *Yunnanodon*, from the Lower Lufeng Formation, are very similar and probably represent sister-taxa by dental apomorphies (Luo pers. comm.). If this taxonomic similarity is taken into consideration, the endemism of tritylodonts would be lower. However, as the stratigraphic position of each formation is not clearly established, definitive palaeogeographical conclusions are very hazardous for that period. The genus *Oligokyphus* has a wide palaeogeographical distribution: remains have been discovered in Germany, the United Kingdom, China and North America. Stratigraphically, it probably ranges from the Rhaetian to the Pliensbachian.

The Upper Elliot and Lower Clarens Formations of southern Africa have yielded three tritheledontid genera. Outside southern Africa, a jaw fragment of the tritheledontid *Pachygelenus* cf. *monus* has been discovered in the ? Hettangian Mc Coy Brook formation of Nova Scotia.

CONCLUSIONS

The Late Triassic cynodont fauna discovered in Saint-Nicolas-de-Port is unique in terms of the diversity of the fauna. The following taxa are represented: *Pseudotriconodon wildi* Hahn, Lepage *et* Wouters, 1984; *Tricuspes tuebingensis* E. von Huene, 1933; *Tricuspes sigogneauae* Hahn, Hahn *et* Godefroit, 1994; *Tricuspes tapeinodon* n.sp.; *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994; *Hahnia obliqua* n.g., n.sp.; *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987; *Lepagia gaumensis*, Hahn, Wild *et* Wouters, 1987; *Maubeugia lotharingica* n.g., n.sp.; *Rosieria delsatei* n.g., n.sp. and aff. *Microscalenodon*. Small carnivorous or insectivorous cynodonts are particularly numerous and diversified (eight species). They are represented by the family Dromatheriidae and by Cynodontia *incertae sedis*. It has been previously shown that Dromatheriidae probably represent the sister-taxon of Mammalia (Hahn *et al.* 1994). Herbivorous cynodonts are rare and probably represented by dwarf forms of the family Traversodontidae. Although very advanced, these traversodonts are characterized by a primitive dental morphology. The study of the palaeogeographical and stratigraphic distribution of Late Triassic to Early Jurassic advanced cynodonts indicates that the fauna discovered in Saint-Nicolas-de-Port is characteristic of the Late Norian-Rhaetian period.

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Les hipparions du gisement miocène supérieur d'Aubignas (Ardèche, France)

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RÉSUMÉ

Dans le gisement d'Aubignas 1, découvert au siècle dernier, coexistent deux espèces d'hipparions : une forme trapue et de taille moyenne, *Hipparion depereti* Sondaar, 1974, bien connue à Montredon (Hérault, France) et une autre espèce de petite taille, *Hipparion* sp., qui rappelle par sa taille *Hipparion macedonicum* Koufos, 1984. Récemment, un nouveau pointement fossilifère, Aubignas 2, très proche du précédent mais légèrement plus haut dans la stratigraphie, a livré une faune assez voisine. Contrairement à Aubignas 1, une seule espèce d'hipparion de grande taille et aux dents brachyodontes existe à Aubignas 2. Elle est apparentée à *Hipparion truyolsi* Sondaar, 1961, signalée aussi aux Mistrals (Vaucluse) et à la Montagne d'Andance (Ardèche). D'après les caractères morphologiques des hipparions, un âge Vallésien supérieur-Turolien inférieur (Miocène supérieur, MN11) est suggéré pour Aubignas 1 et un âge légèrement plus récent, Turolien moyen (MN12), pour Aubignas 2. Le changement de faune entre les deux gisements indique un net changement de paléoenvironnement.

MOTS CLÉS
Miocène supérieur, Aubignas, hipparion, Perissodactyla, Mammalia.

ABSTRACT
The vertebrate fauna of Aubignas 1 discovered during the last century contains two co-existing hipparion species: a medium-sized and robust form, *Hipparion depereti* Sondaar, 1974, well known from Montredon (Hérault, France), and another small species, *Hipparion* sp., which is of similar size to *Hipparion macedonicum* Koufos, 1984. Recently, a new fossiliferous site, Aubignas 2, close to the preceding one, but slightly of higher stratigraphic age, has yielded a similar fauna. Contrary to Aubignas 1, only one large-sized species of hipparion with brachyodont teeth lived in Aubignas 2. It is related to *Hipparion truyolsi* Sondaar, 1961, reported from the Mistrales (Vaucluse) and the Montagne d'Andance (Ardèche). According to the morphological characters of the hipparions, it is suggested that Aubignas 1 is dated to Upper Vallesian-Lower Turolian age, while a slightly younger age, Middle Turolian, is proposed for Aubignas 2.

KEY WORDS
Late Miocene, Aubignas, hipparion, Perissodactyla, Mammalia.

INTRODUCTION

Le gisement d'Aubignas, découvert en 1882 par Torcapel, se trouve à 3 km au nord du village du même nom, dans le département de l'Ardèche. Les fossiles alors exhumés dans ce niveau (Aubignas 1) ont été étudiés par Gaudry qui constate de fortes affinités avec les faunes du Mont Lubéron (Vaucluse, France) et de Pikermi (Grèce). Bout (1966) puis Guerin & Mein (1971) reprennent la liste faunique de Gaudry en la transformant légèrement. Les hipparions ont été signalés sous la dénomination classique d'*Hipparion gracile*. Depuis, Sondaar (1974) a rapproché les équidés d'Aubignas 1 d'*Hipparion depereti*.
Récemment, un nouveau pointement fossilifère (Aubignas 2), très proche du précédent mais situé légèrement plus haut dans la stratigraphie, a livré une faune assez voisine de celle du niveau inférieur (Azanza *et al.* 1993). Les hipparions des deux niveaux d'Aubignas appartiennent à des espèces différentes.

MATÉRIEL, MÉTHODES ET ABRÉVIATIONS

Le matériel d'Aubignas 1 préservé au laboratoire de Paléontologie du Muséum national d'Histoire naturelle comprend un fragment d'hémimandibule avec p2-m2, une vingtaine de dents isolées (surtout des dents jugales supérieures), une extrémité distale de métacarpien principal (Mc III) et deux secondes phalanges.
À Aubignas 2, les hipparions sont représentés par un matériel aussi réduit que celui d'Aubignas 1 : une douzaine de dents isolées, un astragale, un métatarsien principal (Mt III) tronqué au niveau de l'épiphyse distale, trois secondes phalanges et un fragment de scaphoïde.
Les observations et mensurations ont été faites en suivant les recommandations de la Conférence Internationale sur les équidés (Eisenmann *et al.* 1988). Les comparaisons sont faites à l'aide de diagrammes de dispersion pour les dents. L'indice d'hypsodontie de Gromova (1952) rapporte la hauteur maximale du parastyle de dents vierges ou peu usées à la longueur mesurée à 1 cm des racines. L'indice de développement de la quille distale des métapodes centraux a été calculé tel qu'il a été défini par Gromova (1952).

AUBIGNAS 1

COMBIEN D'HIPPARIONS À AUBIGNAS 1 ?

L'unique Mc III incomplet et les deux phalanges intermédiaires ont des dimensions générales et des proportions qui indiquent un hipparion de taille moyenne et d'allure trapue.
Malgré la petitesse de l'échantillon – une douzaine de dents en tout, réparties entre les différentes catégories et appartenant à des stades d'usure différents – les dents jugales supérieures ne sem-

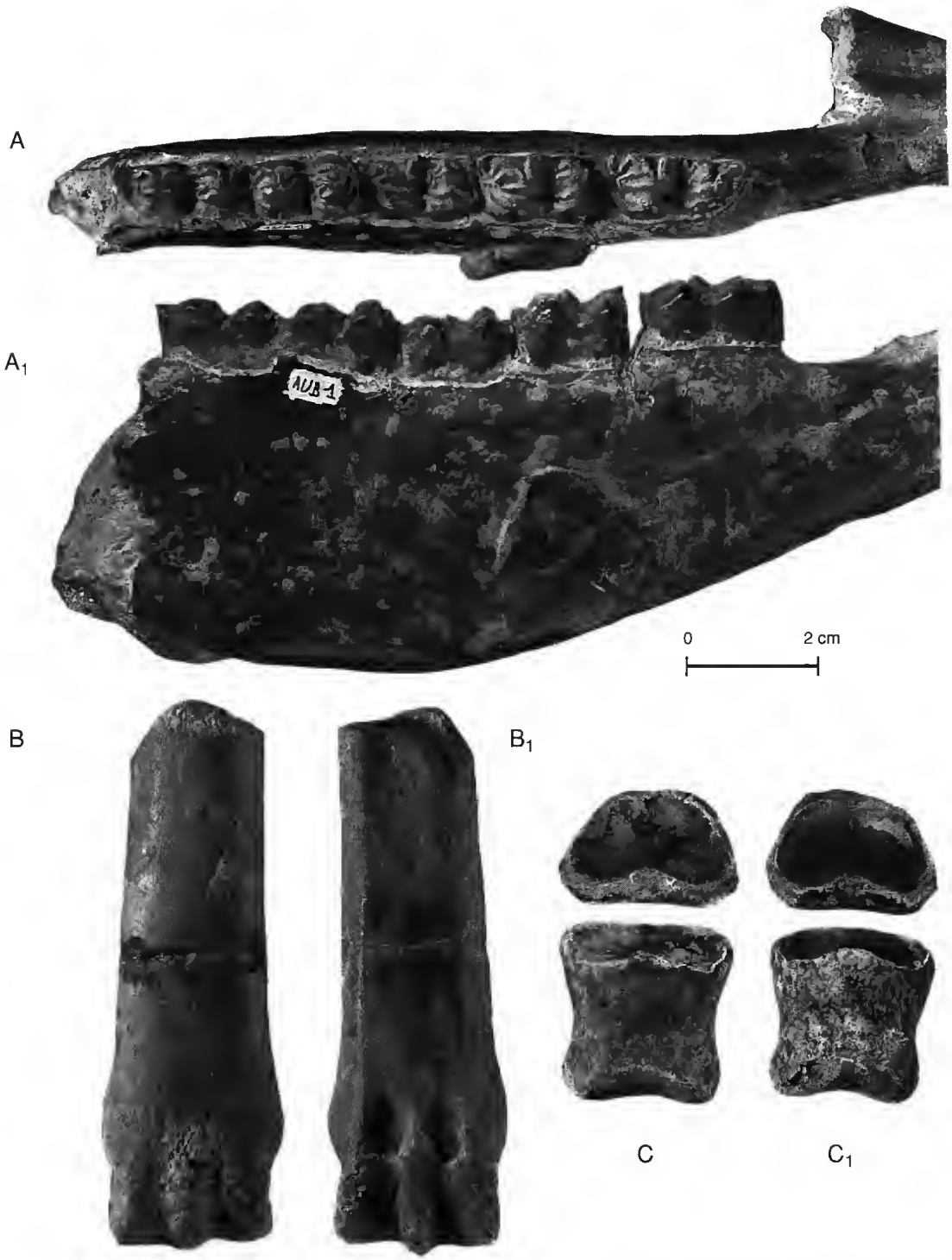


FIG. 1. — *Hipparion depereti*, Aubignas 1. **A-A$_1$**, fragment d'hémimandibule droite n° Aub.1 ; **A**, vue occlusale (p2-m2) ; **A$_1$**, vue vestibulaire. **B-B$_1$**, extrémité distale du Mc III n° Aub 42 ; **B**, vue antérieure ; **B$_1$**, vue postérieure. **C-C$_1$**, Aubignas 1, phalanges intermédiaires principales (Ph II) ; **C**, Ph II n° Aub 40 ; **C$_1$**, Ph II n° Aub 39.

blent pas constituer un échantillon homogène. L'examen des dimensions (Fig. 2), du degré de plissement de l'émail dentaire et d'hypsodontie, de la forme du protocône, etc, permet de faire les constatations suivantes.

1. Une P2 (n° 27) et trois M1 ou M2 (n° 18, 37, 38) se distinguent respectivement des dents de leur catégorie à la fois par des dimensions (longueur et largeur à 1 cm des racines) plus grandes et par un plus fort degré de plissement de l'émail dentaire : vingt-cinq plis pour la P2 de grandes dimensions contre vingt-et-un seulement pour une autre (n° 28) plus petite mais du même stade d'usure qu'elle et vingt-sept à vingt-neuf plis pour deux M1 ou M2 (n° 37, 38), contre seulement vingt pour une P3 ou P4 (n° 25) à peu près de même stade d'usure (en tenant compte, bien sûr, du fait que l'émail dentaire des molaires est un peu plus plissé que celui des prémolaires d'une même série dentaire).

2. Une différence d'hypsodontie est évidente entre d'un côté une M1 ou M2 (n° 18) non usée [l'indice d'hypsodontie (IH) de Gromova (1952) est voisin de 25], classée dans le lot des dents de grandes dimensions, et de l'autre côté deux M1 ou M2 (n° 24, 32) également non usées (IH = 230 et 220), ainsi qu'une P3 ou P4 (n° 22) à peine entamée par l'usure (IH = 190), classées dans le lot des dents à petites dimensions (Tableau 1).

Les dents jugales inférieures sont peu nombreuses et ne permettent pas de relever des différences de dimensions. La double boucle y est typiquement hipparionienne. Un protostylide peut être observé sur toutes les dents mais aucune ne possède d'ectostylide. L'indice d'hypsodontie ne peut-être estimé avec une bonne précision que sur une M1 ou M2 (n° 11). La hauteur de la couronne étant de 48 mm et la longueur à 1 cm des racines, de 22 mm, cet indice devrait être voisin de 220 (Tableau 1).

Sans doute existait-il deux espèces d'hipparions à Aubignas 1, si l'on en juge d'après les dents

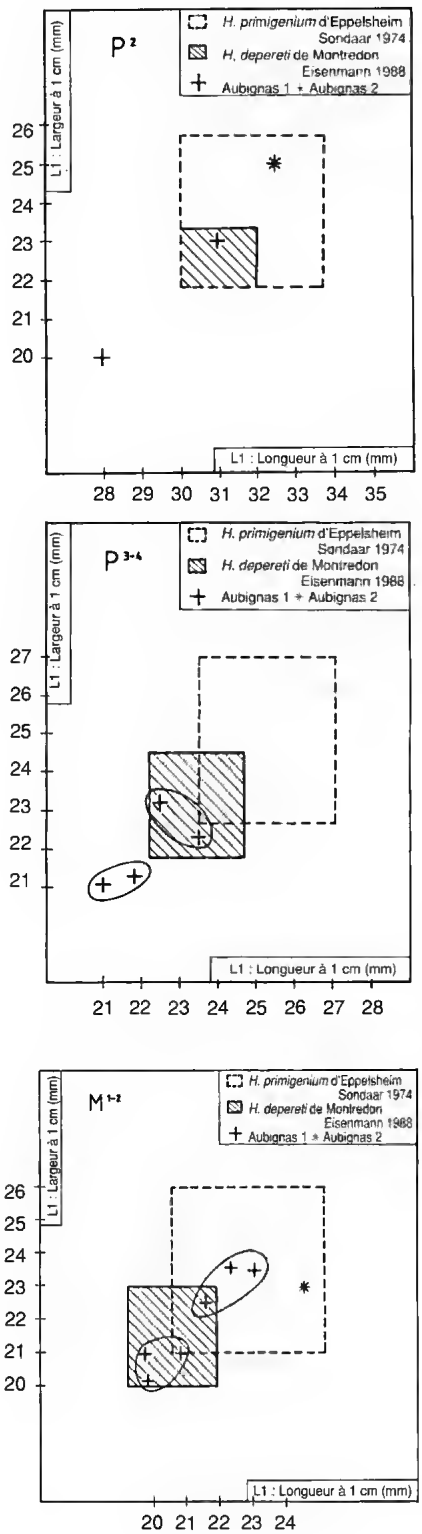
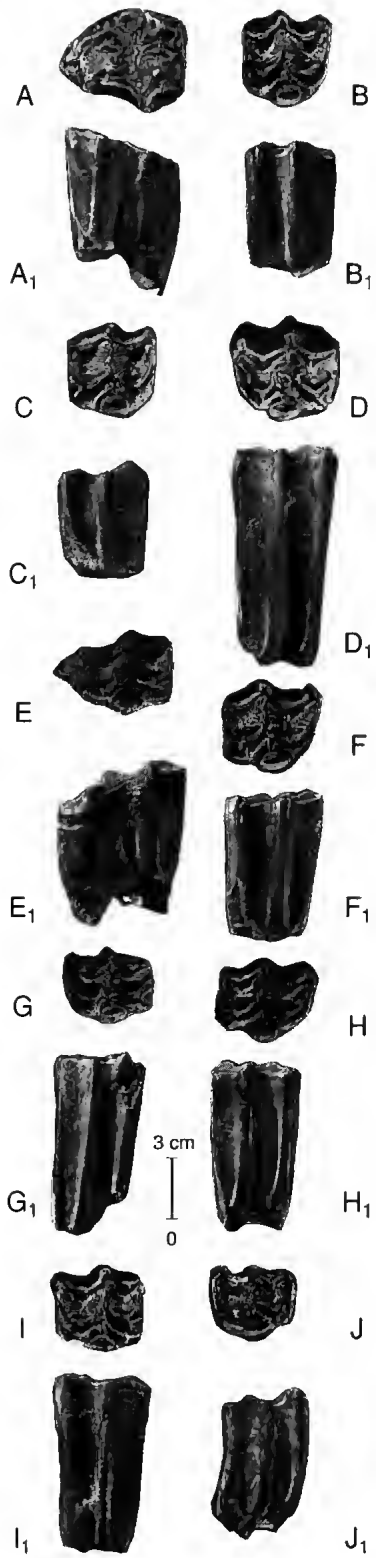


Fig. 2. — Diagrammes de dispersion. **A**, variations des longueurs et des largeurs à 1 cm des racines des deuxièmes prémolaires supérieures (P2) chez des hipparions ; **B**, variations des longueurs et des largeurs à 1 cm des racines des troisièmes et quatrièmes prémolaires supérieures (P3 et P4) chez des hipparions. **C**, variations des longueurs et des largeurs à 1 cm des racines des premières et deuxièmes molaires supérieures (M1 et M2) chez des hipparions.



jugales supérieures. Les quelques os des membres appartiennent à une seule et même forme trapue, ainsi que les dents de plus grandes dimensions, à fort degré de plissement de l'émail dentaire, à hypsodontie moyenne, à protocône ovale et à pli caballin multiple. L'autre espèce possède des dents plus petites, relativement brachyodontes avec un plissement modéré de l'émail dentaire et une constriction de l'hypocône.

Quels hipparions à Aubignas 1 ?

Le matériel d'Aubignas 1 a été rapporté par Sondaar (1974) à *Hipparion depereti*, nouvelle espèce qu'il avait alors créée à Montredon (Hérault, France). Eisenmann (1988) ensuite, s'appuyant sur un matériel un peu plus abondant, a démontré la présence dans ce gisement, en plus d'*Hipparion depereti*, d'un petit hipparion dont la taille évoque *Hipparion macedonicum* du Vallésien supérieur du ravin de la Pluie en Grèce (Koufos 1986). Eisenmann (1988 : 85, 91) a souligné en particulier la ressemblance des dimensions générales du Mc III incomplet d'Aubignas 1 avec ceux d'*Hipparion depereti* et la concordance des dimensions de certaines dents d'Aubignas 1 avec celles des petites dents de Montredon rapportées par elle à *Hipparion* sp.

En effet, il n'y a pas de doute que les quelques os des membres et les dents à fort degré de plissement de l'émail, et à hypsodontie moyenne, appartiennent à *Hipparion depereti* Sondaar, 1974. Le deuxième hipparion d'Aubignas 1 a effectivement des dents jugales semblables à celles de la petite forme de Montredon, mais ni les informations, trop disparates sur ce dernier, ni celles apportées par le matériel d'Aubignas 1 ne permettent d'apparenter ou d'éloigner ces deux hipparions.

Fig. 3. — . **A-D$_1$**, *Hipparion depereti*, Aubignas 1 : dents jugales supérieures. **A-A$_1$**, P2 droite n° Aub 27 ; **A**, vue occlusale ; **A$_1$**, vue vestibulaire. **B-B$_1$**, M1 ou M2 droite n° Aub 37 ; **B**, vue occlusale ; **B$_1$**, vue vestibulaire. **C-C$_1$**, M1 ou M2 droite n° Aub 38 ; **C**, vue occlusale ; **C$_1$**, vue vestibulaire. **D-D$_1$**, M1 ou M2 gauche n° Aub 13 ; **D**, vue occlusale ; **D$_1$**, vue vestibulaire. **E-J$_1$**, *Hipparion* sp. Aubignas 1, dents jugales supérieures. **E-E$_1$**, P2 gauche n° Aub 28 ; **E**, vue occlusale ; **E$_1$**, vue vestibulaire. **F-F$_1$**, P3 ou P4 gauche n° Aub 25 ; **F**, vue occlusale ; **F$_1$**, vue vestibulaire. **G-G$_1$**, M1 ou M2 droite n° Aub 24 ; **G**, vue occlusale ; **G$_1$**, vue vestibulaire. **H-H$_1$**, M1 ou M2 gauche n° Aub 32 ; **H**, vue occlusale ; **H$_1$**, vue vestibulaire. **I-I$_1$**, M1 ou M2 gauche n° Aub 22 ; **I**, vue occlusale ; **I$_1$**, vue vestibulaire. **J-J$_1$**, M3 gauche n° Aub 23 ; **J**, vue occlusale ; **J$_1$**, vue vestibulaire.

AUBIGNAS 2

Combien d'hipparions à Aubignas 2 ?

Les quelques os des membres énumérés précédemment forment un matériel homogène. Ils sont de grandes dimensions, voisines de celles d'*Hipparion primigenium* et plus grandes que celles d'*Hipparion depereti*. Bien qu'incomplet, le Mt III semble appartenir à un hipparion assez robuste : la largeur de la diaphyse au milieu est de 27 mm, qui est aussi la valeur de son diamètre antéro-postérieur au même niveau (respectivement, mesures 3 et 4 d'Eisenmann *et al.* 1988). Sur la surface articulaire proximale existe une petite facette articulaire pour le petit cunéiforme.

Les dents jugales sont peu nombreuses, mais contrairement à celles d'Aubignas 1, elles constituent un échantillon homogène.

Les dents jugales supérieures sont au nombre de six spécimens : trois P2, une P3 ou P4 et deux M1 ou M2. Leurs dimensions sont grandes (Fig. 2) et s'inscrivent à l'intérieur des limites de variation d'*Hipparion primigenium* d'Eppelsheim (Sondaar 1974). Le degré de plissement de l'émail dentaire est cependant plus faible que chez l'hipparion vallésien d'Eppelsheim : vingt ou vingt-et-un plis sur les P2, vingt-cinq plis sur une P3 ou P4 moyennement usée. Les dents sont brachyodontes ; l'indice d'hypsodontie estimé sur une M1 ou M2 à peine entamée par l'usure est de 190. La forme du protocône est ovale sur toutes les dents à partir d'un certain stade d'usure. Le pli caballin est simple ou double.

Les dents jugales inférieures sont au nombre de sept spécimens : deux p3 ou p4, deux m1 ou m2 et trois m3. La double boucle y est typiquement hipparionienne. Le sillon vestibulaire est un peu profond sur les dents peu usées, très profond, entrant même en contact avec le pédoncule de la double boucle sur les dents très usées. Un protostylide est observé sur la plupart des dents entamées par l'usure. Sur une m3 non usée, le protostylide atteint seulement un centimètre environ de hauteur. Aucune dent jugale inférieure définitive ne possède d'ectostylide.

Quel hipparion à Aubignas 2 ?

L'hipparion d'Aubignas 2 diffère de ceux d'Aubignas 1 par sa grande taille et par les caractères morphologiques de ses dents. Les dents jugales supérieures sont plus grandes, à émail dentaire moins plissé et surtout beaucoup plus brachyodontes que celles rapportées à *Hipparion depereti* d'Aubignas 1. Celles d'*Hipparion* sp. sont encore beaucoup plus petites. L'hipparion d'Aubignas 2 a effectivement des dimensions voisines de celles des *Hipparion primigenium* mais se distingue nettement de ces derniers par un moindre degré de plissement de l'émail dentaire des jugales supérieures, et par la forme du protocône, plus arrondie chez l'*Hipparion* d'Aubignas 2. Par ses grandes dimensions, ses dents brachyodontes, la forme de son protocône et le degré de plissement de son émail dentaire, l'hipparion d'Aubignas 2 se rapproche énormément d'*Hipparion truyolsi* Sondaar, 1961 et qu'Alberdi (1974) décrit sous la dénomination subspécifique d'*Hipparion primigenium truyolsi*.

Tableau 1. — Indice d'hypsodontie des hipparions d'Aubignas 1 et 2. IH = indice d'hypsodontie, H = hauteur de la couronne, L1 = longueur de la dent à 1 cm des racines, l1 = largeur de la dent à 1 cm des racines.

N°	catégorie de dent	IH = H/L × 100	L1 × l1 (mm)	Hipparions
Aub 18	M1-2	250	21,5 × 21	*H. depereti*
Aub 11	m1-2	220	22 × ?	–
Aub 24	M1-2	203	19,6 × 20	–
Aub 32	M1-2	220	21 × 19,6	*Hipparion* sp.
Aub 22	P3-4	190	21 × 21	–
Aub 212	M1-2	190	24,5 × 23	*H. truyolsi*

L'ÂGE DES GISEMENTS D'AUBIGNAS

La présence de deux hipparions dans le gisement d'Aubignas 1 pourrait plaider pour un âge turolien puisque la tradition voulait qu'une seule espèce d'hipparion soit présente dans les gisements vallésiens et au moins deux dans le Turolien. Cependant, la coexistence de deux hipparions dès le Vallésien supérieur semble être aujourd'hui bien établie (Koufos 1986 ; Eisenmann 1988). Toutefois, l'âge géologique d'Aubignas 1 et 2 peut être estimé à partir des caractères morphologiques des hipparions.

Le Mc III incomplet et les secondes phalanges d'Aubignas 1 ont des dimensions générales et des

proportions qui les rapprochent de certains hipparions vallésiens, en particulier d'*Hipparion depereti* de Montredon pour lequel Eisenmann (1988) a suggéré un âge Vallésien supérieur-Turolien inférieur. Les dents isolées d'Aubignas 1 posent problème dans la mesure où elles ont été réparties entre deux espèces d'après les différences de leurs dimensions, mais aussi d'après les différences de leurs caractères morphologiques. Si le fort plissement de l'émail dentaire et l'hypsodontie moyenne (biozone 2 des hipparions d'après Sen *et al.* 1978) des dents attribuées à *Hipparion depereti* et la brachyodontie de celles d'*Hipparion* sp. placent Aubignas 1 parmi les

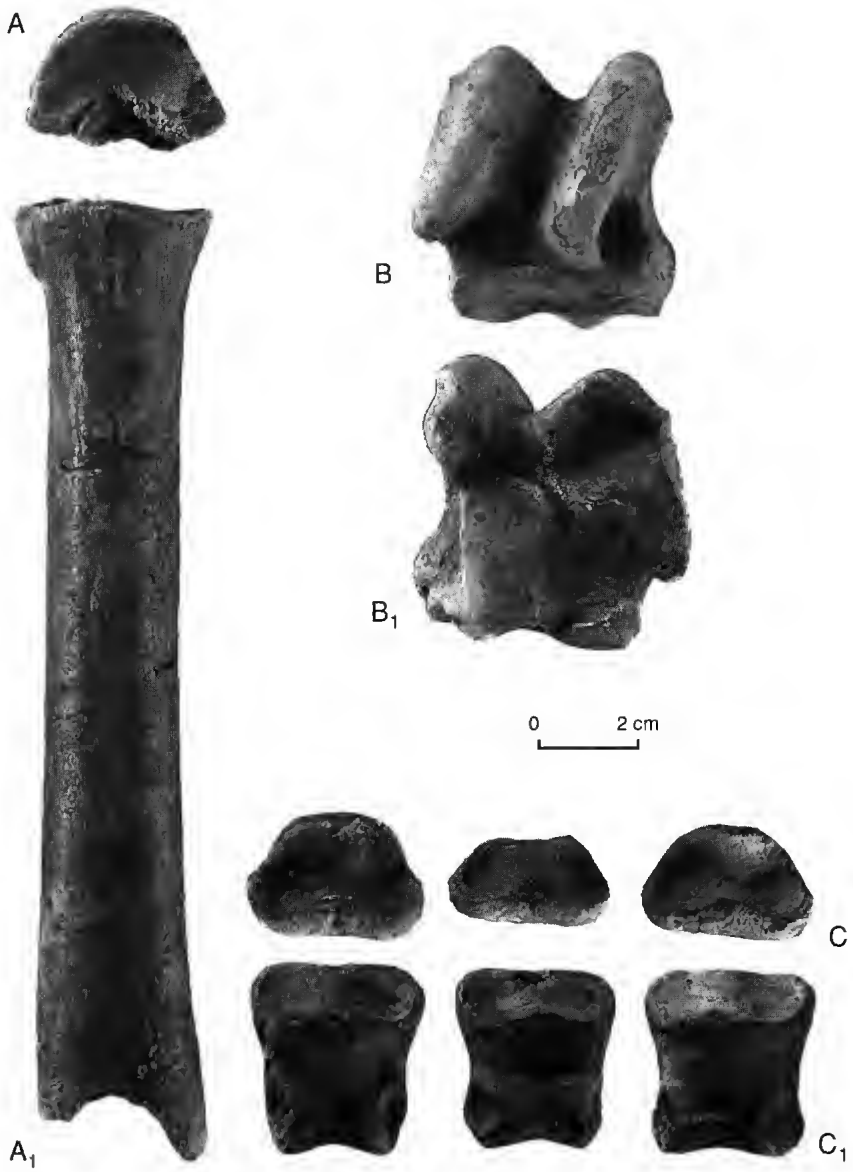


FIG. 4. — *Hipparion truyolsi*, Aubignas 2. **A-A$_1$**, Mt III droit (n° Aub 203) ; **A**, vue de la surface articulaire proximale ; **A$_1$**, vue antérieure. **B-B$_1$**, astragale droit (n° Aub 202) ; **B**, vue antérieure ; **B$_1$**, vue postérieure. **C-C$_1$**, trois secondes phalanges principales (n° Aub 204, 205, 206) ; **C**, vue de la surface articulaire antérieure ; **C$_1$**, vue antérieure.

gisements vallésiens supérieurs, le plissement modéré de l'émail dentaire d'*Hipparion* sp. ainsi que le développement relativement progressif de la quille distale de l'unique Mc III [indice de Gromova (1952) de 91] suggèrent plutôt un âge Turolien inférieur (MN11) pour Aubignas 1.

La morphologie crânienne d'*Hipparion truyolsi* est méconnue. Cette espèce a été définie par Sondaar (1961) d'après les caractères dentaires et sur la base d'un matériel assez réduit. La morphologie dentaire d'*Hipparion truyolsi* ne semble pas être très répandue non plus. En dehors d'El Arquillo en Espagne, localité-type, cette espèce n'a été décrite par la suite que dans le gisement turolien des Mistrals (Vaucluse, France) où elle est une forme rare à côté d'*Hipparion prostylum*, l'espèce la plus commune (Sondaar *et al.* 1977) et dans la Montagne d'Andance en Ardèche (Demarq *et al.* 1988). Un âge Turolien et plus vraisemblablement Turolien moyen (MN12) peut être suggéré pour le gisement d'Aubignas 2. Ce dernier serait par conséquent légèrement plus récent que le niveau d'Aubignas 1. Ces résultats stratigraphiques confirment ceux précédemment avancés par Azanza *et al.* (1993) et établis principalement sur l'étude des artiodactyles.

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Equus stenonis from the middle Villafranchian locality of Volax (Macedonia, Greece)

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ABSTRACT
The locality of Volax is situated in eastern Macedonia, Greece, in a small karstic-tectonic basin. The Volax horse is a large-sized horse with moderately plicated enamel in the upper teeth, short protocone with flat lingual border, hypsodont teeth, slightly plicated flexids in the lower teeth, as well as short and robust metapodials. The dental and postcranial characters of the Volax horse indicate that it is a stenonoid horse with greatest similarities to the horse from Dafnero (Greece) and La Puebla (Spain). It is also close to *E. s. vireti* from Saint-Vallier, as well as to the horse from Olivola and Matassino (Italy). The study of the Volax equid adds to our knowledge about the Villafranchian horses and their relationships. The age of the Volax locality is also discussed and a middle Villafranchian age (MN17) is proposed.

KEY WORDS
mammalia,
Equidae,
middle Villafranchian,
Macedonia,
Greece.

RÉSUMÉ
Le gisement fossilifère de Volax se situe en Grèce, dans la Macédoine orientale. Le matériel d'équidé trouvé dans ce gisement fait l'objet de ce travail. Il s'agit d'un équidé de grand taille, à l'émail de la denture supérieure modérément plissé, doté d'un court protocône et d'une face linguale plate, d'une hypsodontie assez forte. Les flexides de la denture inférieure sont légèrement plissés, les métapodiaux courts et robustes. Ces caractéristiques montrent de fortes similitudes avec *E. s. vireti* des gisements de Dafnero (Grèce) et de La Puebla (Espagne). L'équidé de Volax ressemble aussi à *E. stenonis* de Saint-Vallier, et à l'équidé d'Olivola et de Matassino (Italie). L'étude des équidés de Volax parfait notre connaissance des chevaux du Villafranchien et de leurs relations de parenté. La datation du gisement est également discutée ; un âge Villafranchien moyen (MN17) peut être proposé.

MOTS CLÉS
mammifères,
équidés,
Villafranchien moyen,
Macédoine,
Grèce.

INTRODUCTION

The locality of Volax has been discovered in 1961 by Prof. H. J. Martini (University of Hannover), who investigated the area studying the manganium deposits and informed Prof. O. Sickenberg, of the same University, about the new locality. With the permission of Prof. M. Mitzopoulos (University of Athens) and Prof. G. Matinos (University of Thessaloniki), Sickenberg excavated and collected abundant material which was carried to Hannover (Sickenberg 1968a). Part of the material, including the carnivores and the giraffids, was studied by Sickenberg and then sent back to the University of Athens (Sickenberg 1967, 1968b). The rest material remained in Hannover till 1992. At that time one of us (G. Koufos) asked from the University of Hannover to send back the material. The director of the laboratory in Hannover, Prof. Becker-Platten, sent back immediately to our laboratory the material in his disposal. This material was prepared and registered again. The artiodactyls (bovids and cervids) were given by G. Koufos to D. Kostopoulos and have been studied by him as a part of his thesis (Kostopoulos 1996). The rest material, including the equids, is studied in this article.

The locality is situated near the village of Volax about 11 km north-west of Drama (Fig. 1) in a small karstic-tectonic basin. The basin is filled by clastic sediments belonging to two alluvial fans. The deposits consist of alternating beds of conglomerates and calcareous sandstones with lenticular intercalations of very hard calcitic-arenaceous clays including the fossils. Two fossiliferous sites have been found, referred as Lager 1 and Lager 2 (Sickenberg 1968a). Both sites are situated in Leprokatia ravine; Lager 2 is located at the eastern wall of the ravine and Lager 1 at the western wall, about 3-5 m above Lager 2 (Kostopoulos 1996). The matrix is very hard and the preparation of the fossils quite difficult. The material from both sites was mixed by Sickenberg and for this reason it will be referred as a single sample under the locality indication "Volax" (VOL).

The Volax material includes quite well preserved specimens of equids which allow a good description and comparison with the known

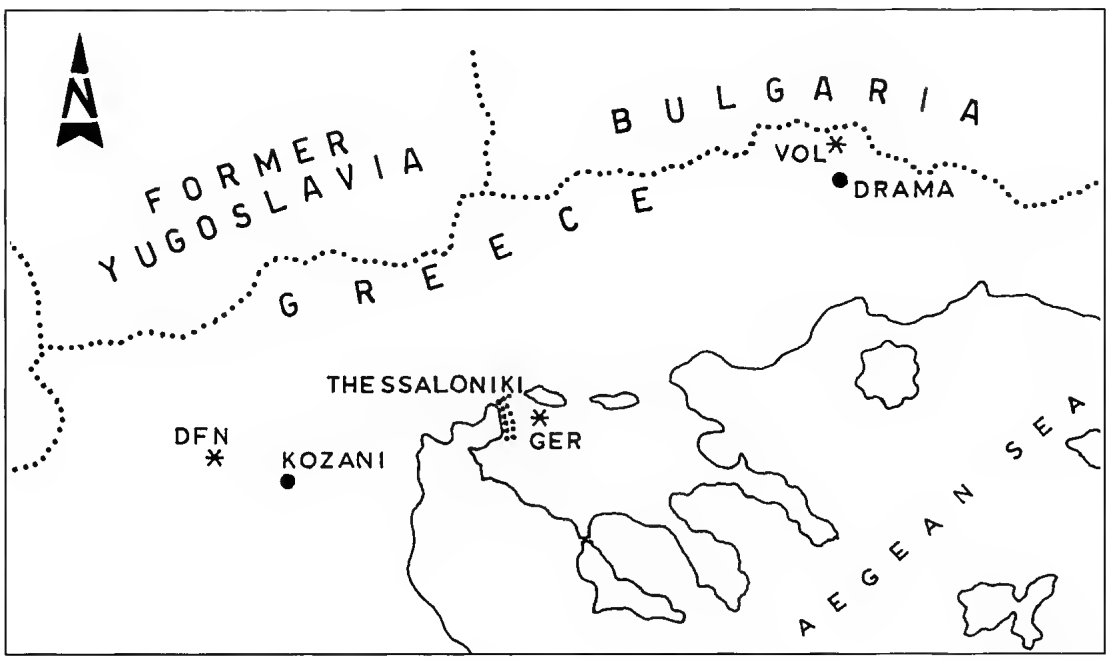

FIG. 1. — Sketch map indicating the various referred Villafranchian localities of Macedonia, Greece.

Villafranchian horses of Greece and Europe: Some years ago the Villafranchian equids of Greece were more or less unknown. Recently a rich sample from the various localities of Mygdonia basin (Macedonia, Greece) has been described (Koufos 1992; Koufos *et al.* in prep.). Some material of Villafranchian horses was also described from western Macedonia, Greece (Steensma 1988; Koufos & Kostopoulos 1993). Moreover some equids are also reported from the Villafranchian locality of Sesklon (Thessaly, Greece) by Symeonidis (1991-1992). The study of the Volax equids will add to our knowledge about the Villafranchian horses and their relationships, as well as to the biostratigraphy of Villafranchian.

The descriptions and measurements of the material are given according to the system proposed by Eisenmann *et al.* (1988).

PALAEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Genus *Equus* Linneaus, 1758
Species ***Equus stenonis*** Cocchi, 1867

Equus stenonis cf. ***vireti***

LOCALITY. — "Volax", VOL (= Lager 1 and 2 of Sickenberg 1968a), Macedonia, Greece.

AGE. — Middle Villafranchian (late Pliocene).

MATERIAL. — Maxilla with P2-M3 dex and P2-M2 sin, VOL-203; P2 dex, VOL-209; P3,4 sin, VOL-207; M3 sin, VOL-208; mandible, VOL-202; right mandibular ramus with dp2-dp4, VOL-204; 5 distal parts of humerus, VOL-172, 173, 174, 175, 177; radius, VOL-170; proximal part of radius, VOL-169; 2 distal parts of radius, VOL-167, 168; 2 Mc III, VOL-152, 155; proximal part of Mc III, VOL-157; 2 distal parts of Mc III, VOL-153, 156; tibia, VOL-162; 2 proximal parts of tibia, VOL-163, 165; 4 distal parts of tibia, VOL-160, 161, 164, 166; os cuboid, VOL-198; 2 astragali, VOL-167, 169; 2 Mt III, VOL-145, 149; 3 proximal parts of Mt III, VOL-144, 146, 147; 5 distal parts of Mt III, VOL-148, 150, 154, 158, 159; first anterior phalanx, VOL-183; first posterior phalanx, VOL-181; proximal part of first phalanx, VOL-184; 2 distal parts of first phalanx, VOL-182, 185; 2 second phalanges, VOL-186, 187; 4 third phalanges, VOL-188, 189, 190, 191.

DESCRIPTION

Maxilla and mandible

A maxilla (Fig. 2) is only known with both toothrows and a more or less complete mandible (Fig. 3) without the ascending ramus. The palate is relatively elongated, narrow and deep. The distance anterior border of P2-choanae is 148 mm, while the palatal breadth is 73.4 mm in front of P2 and 75.5 mm between the posterior borders of P4. The choanae are broad and their anterior border is situated at the middle of M2. The facial crest is strong and its anterior border is situated above M1. The toothrow length is 185 mm and the length of the premolar and molar rows is 102 mm and 83.6 mm respectively. The index Molar length × 100/Premolar length is 83.6 *vs* 88.6 for *E. s.* cf. *vireti* (Dafnero, western Macedonia, Greece), 84.2 for *E. s. mygdoniensis* (Gerakarou, Mygdonia basin, Macedonia, Greece), 84.1 for *E. s.* cf. *vireti* (La Puebla, Spain), 82.7 for *E. s. vireti* (Saint-Vallier, France), 80 for *E. s. senezensis* (Seneze, France) and 76.9-86.2 for *E. s. stenonis* from U. Valdarno; data from Prat (1968), Eisenmann (1980), Privat Defaus (1986), Koufos (1992), and Koufos & Kostopoulos (1993). The Volax horse in this character is similar to the stenonoid horses. In front of P2 there is the trace of a small single-rooted dP1.

The mandible is large and elongated with relatively shallow horizontal ramus. The snout is relatively long and narrow; however at the incisor's area it is wide. The symphysis is elongated. There is not any trace of dp1. The toothrow length is 188.5 mm, while that of the premolars and molars is 92.2-98.3 mm and 91.5 mm respectively. The index Molar length × 100/Premolar length is 93.6 *vs* 92.6 for *E. s.* cf. *vireti* (Dafnero, western Macedonia, Greece), 95.6 for *E. s. mygdoniensis* (Gerakarou, Mygdonia basin, Macedonia, Greece), 92.3 for *E. s. senezensis* (Senèze, France) and 90.3-96.6 for *E. s. stenonis* from U. Valdarno; data from Prat (1968), Privat Defaus (1986), Koufos (1992) and Koufos & Kostopoulos (1993).

Permanent dentition

The upper teeth are small relatively to the skull with strong mesostyle.

The fossettes are always closed and isolated. The enamel in their borders is slightly plicated. In the very worn teeth (VOL-209) the enamel is simple and the fossettes are buccolingually narrow. The plication number is as an average five plis in the premolars and six plis in the molars. The protocone is assymetrical and relatively short with flat lingual border. In the premolars it is triangular, while in the molars it is more elongated and elliptical. In the extremely worn P2 (VOL-209) the protocone is rounded. The short protocone characterizes *E. stenonis* (Azzaroli 1965; De Giuli 1972). The pli cabalin is simple and small or rudimentary. The hypocone is elliptical with rounded distolabial border. The distal hypoconal groove is narrow and shallow, while a slight lingual groove is present only in the premolars. In M3 there is one isolated hypoconal islet. There are no unworn or little worn teeth to measure the hypsodonty but from the available material the teeth seem to be hypsodont.

The lower incisors are medium-sized with elliptical-rounded crowns and well developed cusps. The paraconid is moderately developed in p2. The parastylid is moderately developed; its lingual border does not exceed the middle of the metaconid. It is also closed from all sides, suggesting a "stenonine" type horse (Eisenmann 1981, fig. 3).

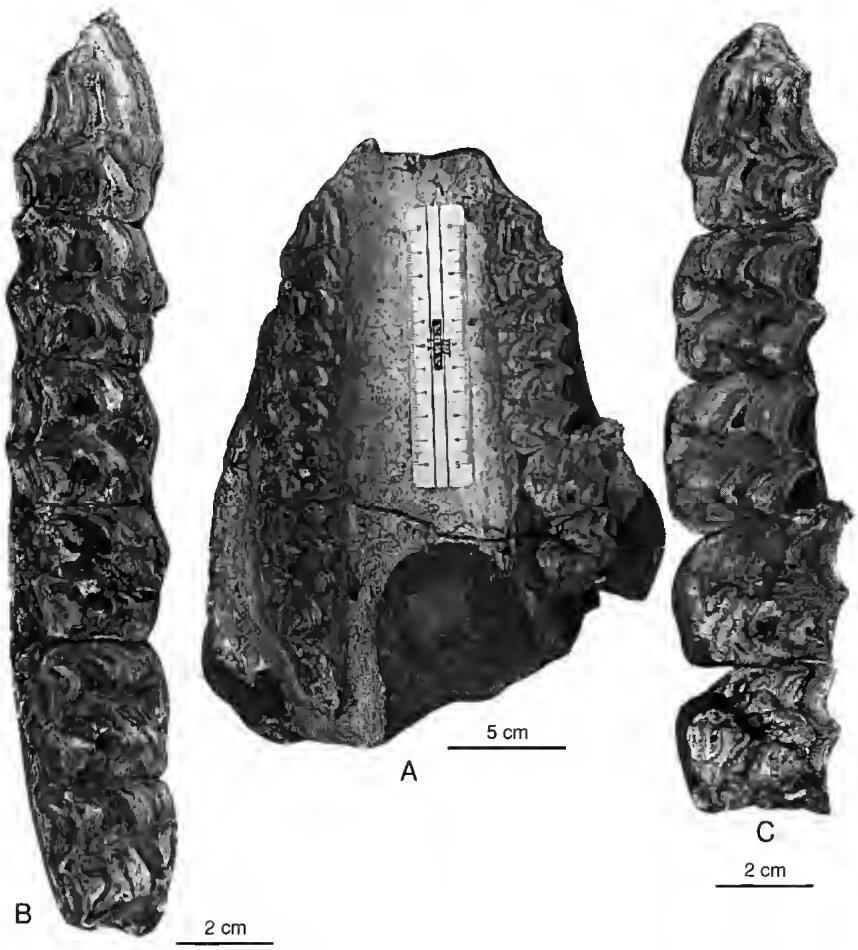

FIG. 2. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. **A**, maxilla with P2-M3 dex and P2-M2 sin, VOL-203; **B**, right toothrow of the maxilla VOL-203; **C**, left toothrow of the maxilla VOL-203.

The metaconid is rounded, the metastylid elliptical-rounded and the entoconid squarish in the premolars and elliptical in the molars. The lingual wall of both metaconid and metastylid is convex. The linguaflexid is V-shaped and deep, like in the "stenonine" type horses (Azzaroli 1965; De Giuli 1972; Eisenmann 1981). The linguaflexid is shallower in the premolars than in the molars; in the latter it sometimes touches the ectoflexid. The latter is V-shaped, open and shallow in the premolars but deeper and narrower in the molars. There is a simple and very small rudimentary pli caballinid which tends to disappear in the more worn teeth (m1 of VOL-208). The enamel at the preflexid' borders is simple, while the postflexid has plicated or crenulated enamel in its buccal border.

Milk dentition

A unique complete lower milk tooth row with slightly worn teeth is available. The paraconid in dp2 is moderately developed. The parastylid in dp3,4 is well developed and closed. The enamel at the flexid's borders is simple, without plications. The linguaflexid has open-V shape, while

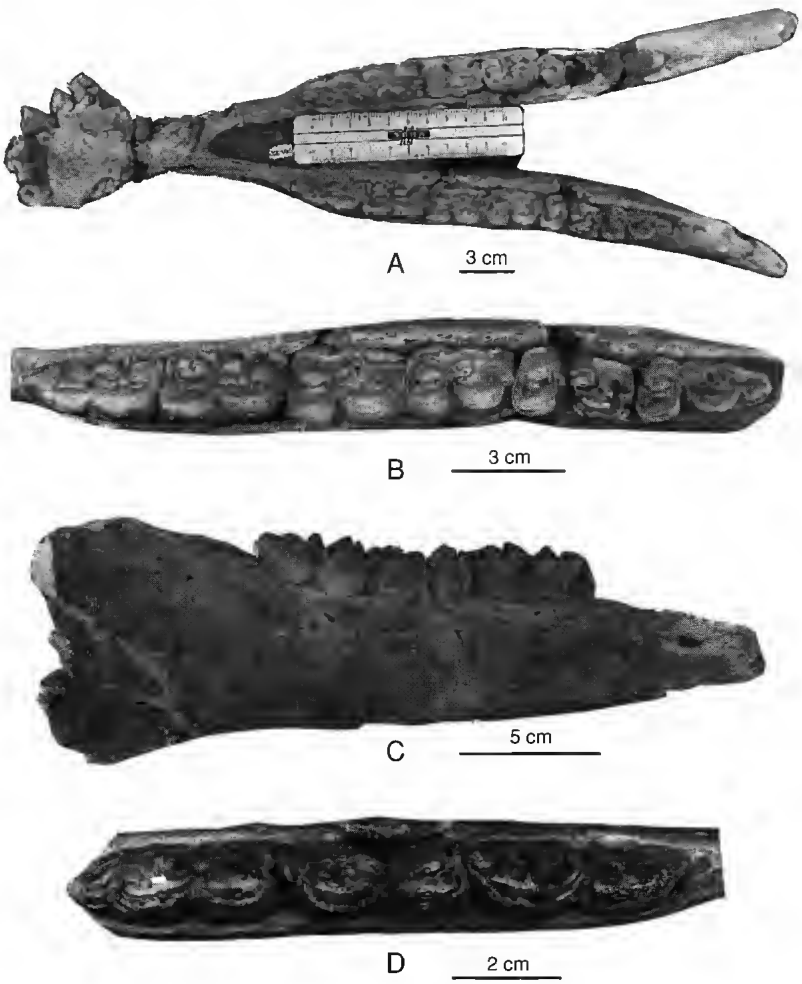

FIG. 3. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. **A**, mandible with both toothrows, VOL-202; **B**, left toothrow of the mandible VOL-202; **C**, right mandibular ramus with dp2-dp4, VOL-204; **D**, right milk toothrow of the mandible VOL-204.

the ectoflexid is narrow, U-shaped and touches the linguaflexid. The metaconid, metastylid and entoconid are little worn and their shape is asymmetrical. The hypoconulid is well developed; in dp3 it is separated as an islet. There is no trace of ectostylid. In front of dp2 there is the alveole of a very small dp1.

Postcranials

The postcranials are few and badly preserved. Nevertheless, there are some complete metapodials, phalanges and some tarsals.

Metacarpals. These are short and robust. The index height Mc III × 100/height Radius is 66.5 and suggests a short metacarpal. The slenderness

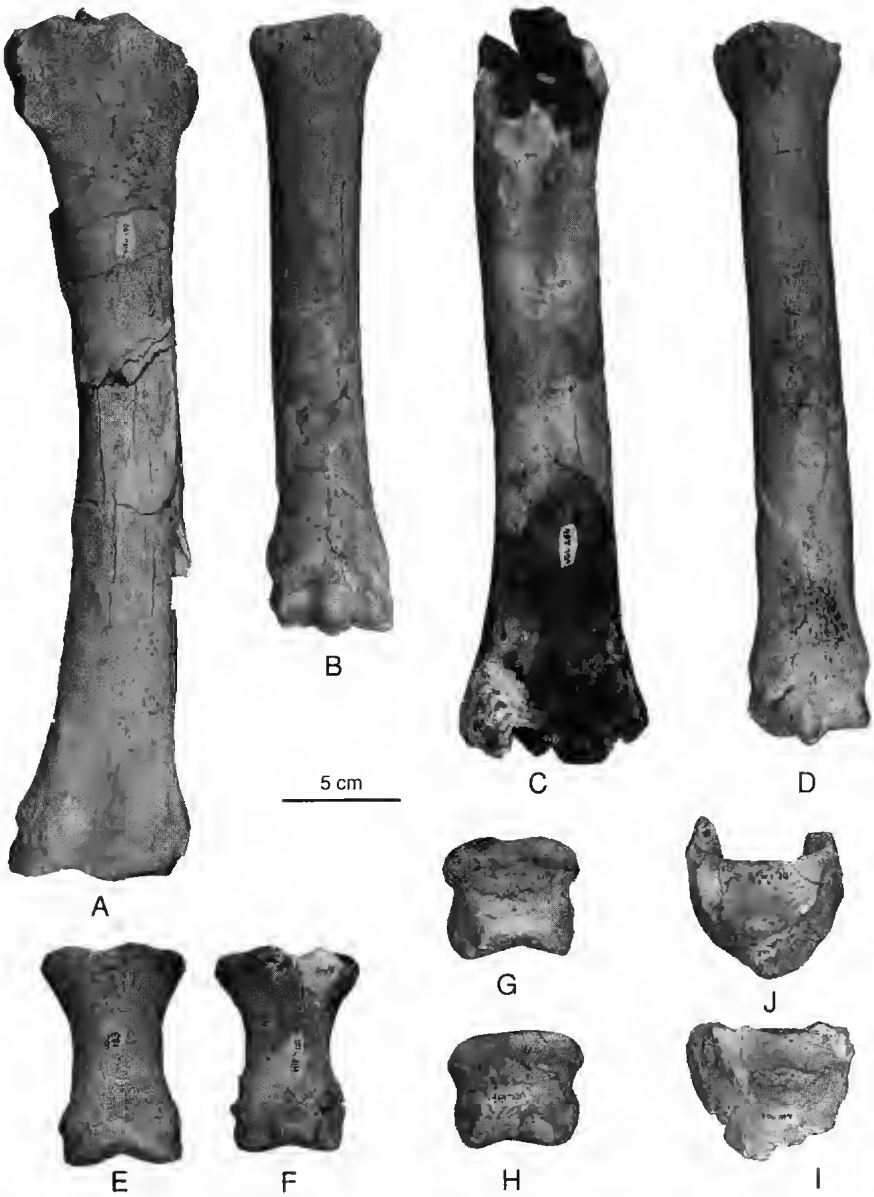

FIG. 4. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. **A**, radius, VOL-170; **B**, third metacarpal, VOL-155; **C**, distal part of tibia, VOL-164; **D**, third metatarsal, VOL-149; **E**, phalanx I anterior, VOL-183; **F**, phalanx I posterior, VOL-181; **G**, phalanx II, VOL-186; **H**, phalanx II, VOL-187; **I**, phalanx III, VOL-189; **J**, phalanx III, VOL-191.

index (= distal articular breadth × 100/height) is 20.1, indicating a relatively robust metapodial. The keel index (= distal articular breadth × 100/max DAP of the keel) is 129.9, indicating a moderately developed keel. In the available metacarpals there is no fusion of the lateral metapodials with the central one, the proximal part is flattened and the anteroposterior diameter of the proximal articular facet is short. The suprarticular fossae are sharp in the anterior face of the distal part with various depth, while in the posterior face the keel is not very high. All these features of the metacarpals are characteristic for the stenonoid horses (Gromova 1949; De Giuli 1972).

Metatarsals. These are short and robust; the slenderness index is 17, indicating a robust metatarsal. Morphologically, in the posterior surface of the distal part, there are two fossae separated by a slight crest indicating a stenonoid horse (De Giuli 1972). In the stenonoid horses the metatarsals relative to the metacarpals are shorter

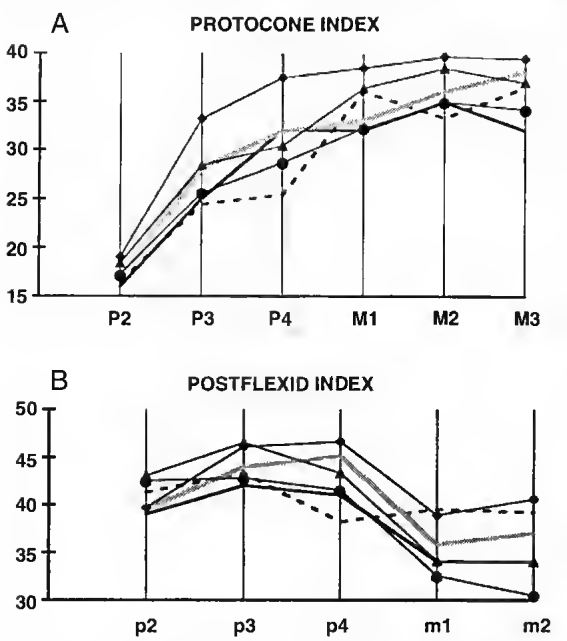

Fig. 5. — Comparative diagram of Protocone index (A) and Postflexid index (B) for the teeth of various stenonoid horses. –, *E. s.* cf. *vireti*, Volax, VOL; –, *E. s* cf. *vireti*, Dafnero, Greece (Koufos & Kostopoulos 1993); , *E. s.* cf. *vireti*, La Puebla, Spain (Eisenmann 1980, 1981); ◆, *E. s. vireti*, Saint-Vallier, France (Eisenmann 1980, 1981); ▲, *E. s. senezensis*, Senèze, France (Eisenmann 1980, 1981); ●, *E. s. mygdoniensis*, Gerakarou, Greece (Koufos 1992).

(De Giuli 1972). The index height Mc III × 100/height Mt III is 87.6, *vs* 84.2 for DFN, 86.5 for La Puebla, 87.8 for Saint-Vallier, 86.5 for Olivola and 87.5-89 for Gerakarou horse. According to this character the Volax equid belongs to the stenonoid horses, as this index for *E. caballus* is 82 (De Giuli 1972).

Astragali. The two available astragali from Volax have higher than 100 index height of the lateral condyle × 100/max breadth; this index is at mean 105 for the Volax equid, while in the caballoid populations it is 96.3 (De Giuli 1972). The crest distinguishing the facets for navicular and cuboid is very sharp and the facet for cuboid is very oblique. These two morphological features suggest a stenonoid horse (Gromova 1949; De Giuli 1972).

First phalanges. These are relatively short and robust; the anterior first phalanx is slenderer than the posterior one. The trigonum phalangis is relatively short; the index max length of trigonum phalangis × 100/height is 56.1 *vs* 70-74 for the caballoid horses (De Giuli 1972). Thus, in this feature, the Volax horse is similar to the stenonoid horses. The second phalanges are short, robust and anteroposteriorly flattened.

DISCUSSION

As referred in the description, the Volax equid has dental and postcranial morphology and proportions similar to those of *E. stenonis*. However there are several subspecies of *E. stenonis* described from various European localities. Two well known subspecies are known from Macedonia: *E. s.* cf. *vireti* from the locality of "Dafnero" (DFN), western Macedonia, Greece (Koufos & Kostopoulos 1993), and *E. s. mygdoniensis* from the locality of "Gera-karou-1" (GER), Mygdonia basin, Macedonia, Greece (Koufos 1992). A stenonoid horse referred as *E. stenonis* is known from Thessaly (Symeonidis 1991-1992). A small-sized stenonoid horse similar to that from Gerakarou is also referred from the Grevena basin as *E. s.* cf. *senezensis* (Steensma 1988). Besides these Greek subspecies there are several others known from the Villafranchian of Italy, France and Spain. The Volax equid will be com-

pared with these in order to find its relationships with them.

The Dafnero horse is a stenonoid one which has great similarities with that from Volax. It is a large-sized horse with moderately plicated enamel in the upper teeth (an average of six plis in the premolars and 6.4 plis in the molars), short protocone with flat lingual border, hypsodont teeth, slightly plicated flexids in the lower teeth, short and robust metapodials (Koufos & Kostopoulos 1993). The protocone index (Fig. 5A) of Volax and Dafnero horse is more or less similar, while the postflexid index (Fig. 5B) of the Dafnero horse is high, suggesting longer postflexid. As the postflexid length depends upon the attrition, and as the specimens from Volax are few (1-2), this difference is possibly not valid. The Volax metapodials are very similar to those of Dafnero (Fig. 6A). In the diagrams of figure 6 their lines are parallel to those of Dafnero horse, suggesting similar size and proportions. Moreover their general proportions are similar to those of the large stenonoid horses confirming their determination to *E. stenonis*. Similar results are also taken from the comparison of the first phalanges (Fig. 7). Thus the horse from Volax is similar to that from the middle Villafranchian locality of DFN and both can belong to the same subspecies.

Another stenonoid horse is known from the locality of Sesklon (Thessaly, Greece). It has large dimensions; the length of the lower toothrow is 191 mm (Symeonidis 1991, 1992). The size of the first phalanges and astragalus are very close to those of the VOL equid. Unfortunately there are no measurements from the metapodials for a comparison with the studied ones; the material of Sesklon is still on study. However from the few available data the Sesklon horse seems to be very close to those of Volax and Dafnero.

The horse of La Puebla (Spain), referred as *E. s.* cf. *vireti*, is a large-sized stenonoid horse, similar to the studied one. The upper toothrow length is 191 mm (Eisenmann 1980) *vs* 185 mm for the Volax equid. The protocone index of the Volax equid is similar to that of the La Puebla horse; only the protocone index of P3 and M3 from Volax is smaller than that of La Puebla (Fig. 5A). The postflexid index of the Volax horse is smaller in p4 and m1,2 than that of La Puebla (Fig. 5B). But as the Volax material is very scanty comparatively to that of La Puebla, this difference is not sufficiently proved. The metapodials and first phalanges of the Volax horse fit very well with those of La Puebla; their size and proportions are the same (Fig. 6). Moreover the various indices calculated for the metapodials of the Volax horse are similar to those for the La Puebla one (see description). Taking in account all the above data, the Volax and La Puebla equids are similar and can be determined to the same subspecies.

The subspecies *E. s. vireti* is known from the locality of Saint-Vallier (France). It is larger than

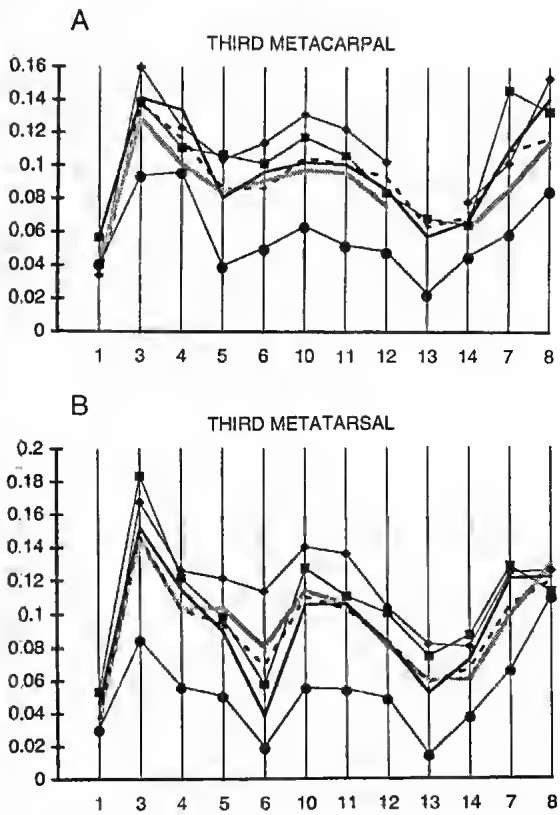

Fig. 6. — Logarithmic ratio diagram comparing the metapodials of the Volax equid with those of *E. stenonis* from various localities. Standard *E. hemionus onager* (Eisenmann & Beckouche 1986). –, *E. s.* cf. *vireti*, Volax, VOL; --, *E. s.* cf. *vireti*, Dafnero, Greece (Koufos & Kostopoulos 1993); . . . *E. s.* cf. *vireti*, La Puebla, Spain (Eisenmann 1979); ◆, *E. s. vireti*, Saint-Vallier, France (Eisenmann 1979); ●, *E. s. mygdoniensis*, Gerakarou, Greece (Koufos 1992); ■, *E. s. stenonis*, Olivola, Italy (De Giuli 1972).

the Volax horse with relatively higher protocone and postflexid indices except those of P2 and p2 (Fig. 5). The toothrow length is 182-196 mm (mean 197.5 mm) for the upper and 176-199 mm (mean 190 mm) for the lower jaw (Prat 1968). The toothrow length of the Volax horse is into the ranges of variation for *E. s. vireti* but its mean values are slightly smaller than those of Saint-Vallier. However the metapodials of *E. s. vireti* have similar height with those from Volax but their proportions are larger, indicating slightly more robust metapodials than those of Volax (Fig. 6). This difference is clearer in the metatarsals. The first phalanx of *E. s. vireti* is also larger than that of Volax (Fig. 7). Considering all these characters the Volax equid has great similarities with the type material of *E. s. vireti* but it is slightly smaller with slightly slenderer metapodials.

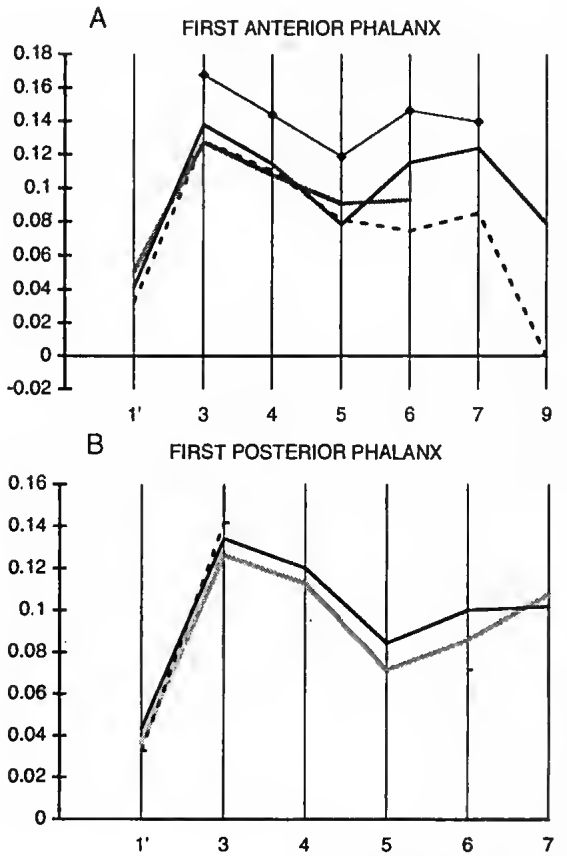

FIG. 7. — Logarithmic ratio diagram comparing the first phalanges of the Volax equid with those of *E. stenonis* from various localities. Standard *E. hemionus onager* (Eisenmann & De Giuli 1974; Dive & Eisenmann 1991). –, *E. s.* cf. *vireti*, Volax, VOL; –. *E.* s. cf. *vireti*, Dafnero, Greece (Koufos & Kostopoulos 1993); –, *E. s.* cf. *vireti*, La Puebla, Spain (Eisenmann 1979). ◆, *E. s. vireti*, Saint-Vallier, France (Eisenmann 1979).

The typical subspecies *E. s. stenonis* is known from the area of Tuscany, Italy (Valdarno, Olivola, Matassino). A good description of this subspecies is given for the material of Olivola and Matassino by De Giuli (1972). The tooth-row length is 187-189 mm for the upper and 194-195 mm for the lower jaw; these values are close to those of the Volax sample. The metapodials from Olivola have slightly larger dimensions than those of Volax, Dafnero and La Puebla, situated between them and *E. s. vireti* from Saint-Vallier (Fig. 6). The maximal diameter of the articular facet for the os magnum in Mc III is significantly longer in the Olivola sample than in the others (measurement 7 in Fig. 6A). The diaphysis is wider in the Olivola metatarsals than in the other horses (measurement 3 in Fig. 6B). *E. s. stenonis* is not very different from *E. s. vireti*; their skull size is similar but *E. s. stenonis* has longer metapodials (Azzaroli 1990). The comparison of the metapodials (Fig. 6) suggests that their general proportions are very similar.

All the European subspecies of *E. stenonis* are based on differences in the size and proportions representing geographical and/or chronological varieties. Sometimes the few available or fragmentary material cannot allow a good statistical analysis evidencing some differences. Three possibilities can be proposed for these large horses of the end of Pliocene: (a) to represent a single subspecies of *E. stenonis* with local varieties; (b) to represent two subspecies, *E. s. vireti* (La Puebla, Dafnero, Volax) and *E. s. stenonis* (Valdarno, Olivola, Matassino); and (c) to include Dafnero, Volax and La Puebla to a new subspecies. The first hypothesis seems to be the most probable but since I have not seen all this material I cannot support it at the moment; a monography revising all European stenonoid horses is necessary in order to clarify their relationships and to define the valuable species and subspecies.

From the Villafranchian localities of Mygdonia basin (Macedonia, Greece), a stenonoid horse has

been described as *E. s. mygdoniensis*; the better sample is that of the locality of "Gerakarou 1", GER (Koufos 1992). *E. s. mygdoniensis* is smaller, with relatively slenderer metapodials than the Volax horse. The toothrow length is 173.5 mm for the upper and 167.8 mm for the lower jaw *vs* 185 mm and 188.5 mm for the Volax horse respectively. The slenderness index is 18.6 for Mc III and 15.9 for Mt III, while in the Volax horse it is respectively 20.1 and 17. The metapodials of the Gerakarou horse have more or less similar height but their relative proportions are quite smaller than those of the studied equid (Fig. 6). The horse found in the locality of Livakos (Grevena basin) and described as *E. s.* cf. *senezensis* (Steensma 1988) is smaller than that of Volax and closer to *E. s. mygdoniensis* (Koufos 1992).

Concerning all the above mentioned descriptive and comparative data, the Volax horse belongs to *E. stenonis* and has greatest similarities with the forms from Dafnero and La Puebla. It is also close to *E. s. vireti* from Saint-Vallier. It has as well some similarities to *E. s. stenonis* from Olivola and Matassino. Thus, the Volax horse is referred as *E. s.* cf. *vireti*.

BIOCHRONOLOGY

The Volax horse belongs to the large-sized stenonoid horses which appeared at the end of Pliocene. The oldest representative of *Equus* in Europe is *E. livenzovensis* while the first appearence of the genus in Eurasia has been dated at about 2.5 Ma (Lindsay *et al.* 1980; Bonadonna & Alberdi 1987). *E. stenonis* including the late Pliocene-early Pleistocene horses with several forms, allowed the subdivision of that time span (Bonadonna & Alberdi 1987; Azzaroli 1990). The Volax horse has some similarities with *E. s. vireti* from Saint-Vallier. The Saint-Vallier locality has been dated to late Pliocene, MN17 (Mein 1990). According to Torre *et al.* (1992) the Saint-Vallier locality belongs to the Saint-Vallier Faunal Unit corresponding to the end of middle Villafranchian. The horse of Volax is very similar to that of Dafnero (Greece) and La Puebla (Spain). The Dafnero locality has been dated to middle Villafranchian (zone MN17a of Mein 1990; or MNQ17 of Guerin 1990), (Koufos *et al.* 1991; Koufos 1993; Koufos & Kostopoulos 1993; Kostopoulos & Koufos 1994; Kostopoulos 1996). The locality of La Puebla is also dated to middle Villafranchian, MN17 and is considered slightly younger than that of Saint-Vallier (Mein 1990). Taking into account the above mentioned similarities of the Volax horse with those from

FAUNA	VOL	DFN	PUE	STV	OLI
Macaca cf. *florentina*			sp.	+	
Paradolichopithecus arvernensis			+		
Anancus arvernensis				+	
Archidiskodon meridionalis			+	+	+
Elephantidae indet.	+				
Nyctereutes megamastoides	+	+	+	+	
Vulpes alopecoides		+	+	+	
Vulpes praecorsac	+				
Canis cf. *falconeri*			+		
Canis etruscus					+
Ursus etruscus		+	+	+	+
Bosfagius felinus	+				
Pliohyaena perrieri			+	+	
Pliohyaena brevirostris					+
Baranogale helbingi		cf.	+		
Chasmaporthetes lunensis		+	+	+	+
Megantereon megantereon	+		+	+	+
Lynx issiodorensis	?			+	+
Acinonyx pardinensis			+	+	+
Panthera schaubi			cf.	+	
Panthera gombaszoegensis					+
Meles thorali				+	
Enhydrictis ardea				+	+
Homotherium sainzelli				+	
Homotherium crenatidens					+
Equus stenonis vireti	cf.	cf.	cf.	+	
Equus stenonis stenonis					+
Dicerorhinus etruscus			+	+	+
Rhinocerotidae indet.	+				
Sus strozzii					+
Mitilanotherium martinii	+	+			
Eucladoceros senezensis	+	+	+	+	
Eucladoceros dicranios					+
"*Cervus*" *philisi*	+	+	+	+	
Croizetoceros ramosus	+		+	+	
Leptobos stenometopon				+	
Leprobos etruscus					+
Leptobos	cf.				
Gazellospira torticornis	cf.	+	+	+	
Gallogoral meneghinii	+	cf.	cf.	+	+
Gazella bouvraint n.sp.	sp.	+			
Gazella borbonica			+	+	
Procamptoceras brivatense	? sp.				+
Antilopinae indet.		+			

FIG 8. — Faunal list: **VO**, Volax (Sickenberg 1967, 1968a, b; Kostopoulos 1996); **DFN**, Dafnero (Koufos 1993; Koufos & Kostopoulos 1993, 1997; Kostopoulos 1996); **PUE**, La Puebla (Aguirre & Morales 1990), **STV**, Saint-Vallier (Heintz *et al.* 1974), **OLI**, Olivola.

Simpson's Index	VOL		DFN		PUE		STV		OLI	
VOL	100	100	75	62	77	63	85	63	39	31
DFN			100	100	91	69	83	69	41	23
PUE					100	100	86	90	57	35
STV							100	100	88	45
OLI									100	100

Pickford's Index	VOL		DFN		PUE		STV		OLI	
VOL	0	0	8	19	8	23	85	63	43	52
DFN			0	0	4	18	10	14	41	65
PUE					0	0	6	3	13	43
STV							0	0	4	36
OLI									0	0

FIG. 9. — Faunal similarities indices of Simpson and Pickford, calculated for the localities of figure 8. The left number is at generic level and the right number at specific level.

the other localities, a similar age can be proposed for the locality of Volax.

The material collected from Volax has been determined by Sickenberg (1967, 1968a, b) and the following species are referred: *Megantereon megantereon megantereon*, *Nyctereutes megamastoides megamastoides*, *Vulpes praecorsac*, *Bosdagius felinus*, *Felis* (*Lynx*) *issiodorensis*?, *Macedonitherium martinii*, *Leptobos* sp., *Nemorhedus* sp., *Gazella* sp., *Gazellospira* sp., *Didermoceros* sp., *Equus* (*Allohippus*) sp. and *Proboscidea* indet., while an earliest Pleistocene age has been proposed. However the presence of *Nyctereutes* in the Volax fauna suggests an older age; the genus has been replaced by *Canis* at the beginning of late Villafranchian (Torre *et al.* 1992). Thus the Volax fauna must be older than Early Pleistocene. The recent study of the bovids and cervids from Volax (Fig. 8) and their comparison with those of the other Greek and European localities suggest also a middle Villafranchian (MN17a) age (Kostopoulos & Koufos 1994; Kostopoulos 1996). This age confirms the above mentioned age proposed for the studied equid.

As it was referred before, the Volax equid is similar or has similatities with that from Dafnero, La Puebla, Saint-Valliet and Olivola. A comparison of the whole fauna from Volax with those of the above mentioned localities is necessary to establish these similarities.The faunal composition of Volax is similar to that of Dafnero, La Puebla and Saint-Vallier (Fig. 8). The similarity index of Simpson is high, both in generic and specific level, while the distance index of Pickford is small (Fig. 9), indicating strong faunal similarities. The differences in the faunal composition are referred in the absence of some small carnivores (Fig. 8), which are difficult to be preserved pre- and post-mortem. Taxonomical ptoblems cause also some differences in the composition of the fauna. The utsid *Bosdagius* is known only from Volax and possibly represents a form of the genus *Ursus*.

However the Olivola fauna differs more from the others and seems to be younger. The Simpson index is small and the Pickford index is high both in generic and specific level indicating the differentiation of the Olivola fauna from the others (Fig. 9). The presence of *Canis etruscus*, *Pliohyaena brevirostris* and *Panthera gombaszoegensis* indicates a younger age for the Olivola fauna. As mentioned before, *Canis etruscus* corresponds to the beginning of early Pleistocene (Torre *et al.* 1992). The large-sized *Pliohyaena brevirostris* appeared in Europe at early Pleistocene in Olivola fauna (Torre *et al.* 1992). However, in Greece, this species has appeared earlier in the Gerakarou fauna, where it was found togethet with *Pliohyaena perrieri*. The Gerakarou fauna has been dated at the transition between Pliocene/Pleistocene (Koufos 1992; Kostopoulos 1996). *Panthera gombaszoegensis* also characterizes the beginning of late Villafranchian (Azzaroli *et al.* 1988) and its presence in the

Olivola fauna indicates a younger age than that of Volax, Dafnero, La Puebla and Saint-Vallier. In the last two localities the more primitive *Panthera schaubi* is present. The Volax fauna preserves more primitive characters and corresponds to Saint-Vallier Faunal Unit of Torre *et al.* (1992). These faunal similarities of the Volax material with the other localities reflect also age similarities and a middle Villafranchian age is proposed for the locality of Volax.

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APPENDIX

MEASUREMENTS AND STATISTICS

Mandible	VOL-202	VOL-204*
2	~156	-
3	95.2	-
4	91.5	-
5	188.5	110.5
7	70	-
10	110	57.7
11	79.5	-
12	63.7	37.2
13	93	-
14	{24}	-
16	140	-

TABLE 1. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Mandible. *, VOL-204 is a hemimandible with milk teeth. **2**, muzzle length: middle of the line connecting the anterior borders of p2 to a point situated between the two i1; **3**, premolar length (alveolar); **4**, molar length (alveolar); **5**, toothrow length (alveolar); **7**, muzzle breadth: breadth at the posterior borders of i3; **10**, height of the jaw behind m3; **11**, *idem* between p4 and m1; **12**, *idem* in front of p2; **13**, symphysis length; **14**, minimal breadth of the symphysis; **16**, length of diastema p2-i3.

		VOL-203		VOL-209
		dex	sin	
P2	Lo	41.8	39.6	41.3
	Bo	27.8	28.0	28.2
	Lp	6.8	6.3	6.4
	Bp	5.7	5.4	5.8
	PI	16.3	15.9	15.5
P3	Lo	30.4	30.8	-
	Bo	27.3	28.7	-
	Lp	7.7	7.6	-
	Bp	6.0	5.4	-
	PI	25.3	24.7	-
P4	Lo	29.5	29.8	-
	Bo	-	29.5	-
	Lp	-	9.4	-
	Bp	-	5.2	-
	PI	-	31.5	-
M1	Lo	26.4	29.0	
	Bo	-	29.2	
	Lp	-	8.4	
	Bp	-	5.0	
	PI	-	29.0	
M2	Lo	26.9	{30.4}	
	Bo	-	27.4	
	Lp	9.6	-	
	Bp	4.4	-	
	PI	35.7	-	
M3	Lo	31.4	-	
	Bo	23.3	-	
	Lp	10.0	-	
	Bp	3.3	-	
	PI	31.8	-	

TABLE 2. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Upper permanent cheek teeth. **Lo**, occlusal length; **Bo**, occlusal breadth; **Lp**, protocone length; **Bp**, protocone breadth; **PI**, protocone index.

		VOL-202	
		dex	**sin**
p2	Lo	37.5	36.5
	Bo ant.	14.2	13.1
	Bo post.	16.7	17.0
	Lprfl	9.0	9.0
	Lptfl	15.0	13.5
	IF	40.0	37.0
p3	Lo	31.2	31.2
	Bo ant.	17.7	18.4
	Bo post.	17.4	19.0
	Lprfl	9.4	9.8
	Lptfl	12.4	13.4
	IF	39.7	42.9
p4	Lo	30.5	29.6
	Bo ant.	17.0	17.8
	Bo post.	17.4	19.0
	Lprfl	9.4	9.2
	Lptfl	12.2	12.6
	IF	40.0	42.6
m1	Lo	28.0	27.7
	Bo ant.	17.4	17.0
	Bo post.	16.8	18.2
	Lprfl	7.6	7.8
	Lptfl	9.0	9.8
	IF	32.1	35.4
m2	Lo	-	30.0
	Bo ant.	-	16.2
	Bo post.	-	-
	Lprfl	-	7.8
	Lptfl	-	10.1
	IF	-	33.7
m3	Lo	-	33.3
	Bo ant.	-	15.8
	Bo post.	-	13.6
	Lprfl	-	7.4
	Lptfl	-	9.4
	IF	-	28.2

TABLE 3. — *Equus stenoni* cf. *vireti*, Volax, Macedonia, Greece. Lower permanent cheek teeth. **Lo**, occlusal length; **Bo ant.**, anterior occlusal breadth; **Bo post.**, posterior occlusal breadth; **Lprfl**, preflexid length; **Lptfl**, postflexid length; **IF**, postflexid index.

Humerus	n	x	min	max	s	v
3	2	37.05	36.5	37.6	0.78	2.10
4	2	45.60	44.9	46.3	0.99	2.17
7	2	82.50	81.0	84.0	2.12	2.57
8	4	87.53	85.2	89.6	2.35	2.69
9	3	50.17	47.2	52.7	2.78	5.53
10	1	40.00	-	-	-	-
11	3	44.73	43.1	46.5	1.70	3.81

TABLE 4. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Humerus. **3**, minimal breadth (oblique); **4**, diameter perpendicular to and at the level of 3; **7**, maximal breadth of the trochlea; 8, distal maximal depth; **9**, maximal trochlear height (medial); **10**, minimal trochlear height (in the middle); **11**, trochlear height at the sagittal crest (near the condyle).

Radius	n	x	min	max	s	v
1	1	362.80	-	-	-	-
2	1	343.00	-	-	-	-
3	3	44.10	43.9	44.4	0.26	0.60
4	3	30.50	28.5	33.0	2.29	7.51
5	1	75.70	-	-	-	-
6	1	[36]	-	-	-	-
7	1	80.90	-	-	-	-
8	2	65.95	65.4	66.5	0.78	1.18
9	1	39.30	-	-	-	-
10	2	78.65	78.1	79.2	-	-
11	2	25.50	25.0	26.0	-	-
12	1	16.90	-	-	-	-

TABLE 5. — *Equus stenoni* cf. *vireti*, Volax, Macedonia, Greece. Radius. **1**, maximal length; **2**, medial length; **3**, minimal breadth of diaphysis; **4**, DAP of the diaphysis at the level of 3; **5**, proximal articular breadth; **6**, proximal articular DAP, **7**, proximal maximal breadth; **8**, distal articular breadth; **9**, distal articular DAP; **10**, distal maximal breadth; **11**, diameter of the articular facet for navicular; **12**, *idem* for triquetrum.

Mc III	n	x	min	max	s	v
1	2	241.45	236.4	246.5	-	-
2	1	241.70	241.7	241.7	-	-
3	2	35.85	35.5	36.2	-	-
4	2	28.70	28.3	29.1	-	-
5	1	52.00	-	-	-	-
6	1	33.80	-	-	-	-
7	1	44.00	-	-	-	-
8	1	17.00	-	-	-	-
9	1	7.50	-	-	-	-
10	3	48.93	47.4	50.0	1.12	2.27
11	4	48.55	47.4	49.7	1.10	2.27
12	3	35.80	33.9	37.2	1.39	3.90
13	3	27.53	27.0	27.9	0.38	1.40
14	4	30.18	29.1	31.5	0.91	3.03
16	2	8.00	7.5	8.5	-	-

TABLE 6. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Third metacarpal. **1**, maximal length; **2**, internal length; 3, breadth of the diaphysis (in the middle); **4**, DAP, *idem* at the level of 3; **5**, proximal articular breadth; **6**, proximal articular DAP; **7**, maximal diameter of the articular facet for os magnum; **8**, diameter of the anterior facet for hamatum; **9**, diameter of the articular facet for Mc II; **10**, distal maximal supra-articular breadth; **11**, distal maximal articular breadth; **12**, distal maximal DAP of the keel; **13**, distal minimal DAP of the lateral condyle; **14**, distal maximal DAP of the medial condyle; **16**, diameter for the articular facet for Mc III.

Tibia	n	x	min	max	s	v
3	3	46.80	45.4	47.7	1.00	2.14
4	3	32.63	31.3	33.5	0.96	2.93
5	1	74.1	-	-	-	-
6	1	61.1	-	-	-	-
7	3	71.23	68.5	75.9	3.32	4.66
8	3	47.00	44.3	49.2	2.03	4.32
9	1	17.0	-	-	-	-

TABLE 7. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Tibia. 3, minimal breadth of the diaphysis; **4**, DAP of the diaphysis at the level of 3; **5**, proximal maximal breadth; 6, proximal maximal depth; **7**, maximal distal breadth; **8**, maximal distal DAP; 9, length of the fossa digitalis.

Astragalus	VOL-196	VOL-197
1	-	65.8
2	-	[63.2]
3	30.6	28.8
4	66	64.7
5	51.3	[55.5]
6	36	34.5
7	48.5	51

TABLE 8. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Astragalus. **1**, maximal length (height) articulation surface for navicular-top of the internal condyle; **2**, maximal diameter of the internal condyle; **3**, trochlear breadth: middle of the internal-middle of the external condyles; **4**, maximal breadth (in projection), **5**, distal articular breadth; **6**, distal articular DAP; **7**, maximal DAP of the internal condyle.

Mt III	n	x	min	max	s	v
1	2	275.50	270.0	281	-	-
3	5	35.60	33.7	37.3	1.31	3.68
4	5	32.94	31.4	34.6	1.14	3.46
5	3	49.80	47.0	52	2.55	5.13
6	2	38.25	38.0	38.5	-	-
7	2	47.50	47.4	47.6	-	-
8	5	11.50	10.7	11.9	0.47	4.12
9	1	6.4	-	-	-	-
10	6	48.70	47.3	50	1.11	2.29
11	6	47.65	46.2	49.5	1.31	2.75
12	7	36.44	34.5	37.9	1.16	3.2
13	6	26.72	25.4	27.5	0.82	3.08
14	5	30.94	29.3	31.7	0.97	3.12

TABLE 9. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Third metatarsal. **1**, maximal length; **3**, breadth of the diaphysis (in the middle); **4**, DAP *idem* at the level of 3; **5**, proximal articular breadth; **6**, proximal articular DAP; **7**, maximal diameter of the articular facet for the cuneiform; **8**, diameter of the articular facet for cuboid; **9**, *idem* for cuneiform II; **10**, distal maximal supra-articular breadth; **11**, distal maximal articular breadth; **12**, distal maximal DAP of the keel; **13**, distal minimal DAP of the lateral condyle; **14**, distal maximal DAP of the medial condyle.

Phalanx I	VOL-181	VOL-182	VOL-183	VOL-184	VOL-185
1	78.4	-	84.6	-	81.8
2	71.4	-	74.9	-	-
3	32.5	-	33.5	-	34.2
4	55.7	-	54.2	44.7	54.6
5	37.0	-	37.4	29.3	-
6	44.1	43.0	46.2	-	47.1
7	42.1	-	45.0	-	46.4
8	23.7	-	24.4	-	25.2
9	42.0	-	50.1	-	45.5

TABLE 10. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. First phalanx of the third digit. **1**, maximal length; **2**, anterior length: middle of the proximal articular facet-middle of the distal facet; **3**, minimal breadth of the diaphysis; **4**, proximal breadth; 5, proximal DAP; **6**, distal breadth at the tuberosities; **7**, distal articular breadth; **8**, distal articular DAP; **9**, minimal length of the trigonum phalangis.

Phalanx II	VOL-186	VOL-187
1	48.6	46.7
2	34.3	33.2
3	45.4	45.2
4	53.8	52.2
5	33.6	32.7
6	49.5	48.1

TABLE 11. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Second phalanx of the third digit. **1**, maximal length; **2**, anterior length (as in the first phalanx); **3**, minimal breadth of the diaphysis; **4**, maximal proximal breadth; **5**, proximal DAP; 6, distal articular maximal breadth.

Phalanx III	VOL-188	VOL-189	VOL-190	VOL-191
1	57.3	47.8	-	55.7
2	47.8	50.5	-	49.8
3	67.3	67.3	-	-
6	37.1	41.4	38.8	40.8

TABLE 12. — *Equus stenonis* cf. *vireti*, Volax, Macedonia, Greece. Third phalanx of the third digit. **1**, length from the posterior edge of the articular surface to the tip of the phalanx; **2**, anterior length; 3, maximal breadth; 6, maximal height.

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